Vol. 17, No. 1 May 1948

THE JOURNAL OF ANIMAL ECOLOGY

MMONWEALTH INST.
TOMOLOGY LIBRARY
OSEP 1948
RIAL Eu.431
PARATE

EDITED FOR THE
BRITISH ECOLOGICAL SOCIETY

by
CHARLES ELTON
and
DENNIS CHITTY

CAMBRIDGE UNIVERSITY PRESS
CAMBRIDGE, AND BENTLEY HOUSE, LONDON
CANADA AND INDIA: MACMILLAN

Annual subscription: thirty-five shillings (twenty-five shillings to members of the British Ecological Society)
Single numbers: twenty-two shillings and sixpence

World-List abbreviation: J. Anim. Ecol.

THE JOURNAL OF ANIMAL ECOLOGY

Vol. 17, No. 1 May 1948

CONTENTS

PAGE

P. H. T. Hartley. Food and feeding relationships in a community of fresh-water fishes 1

L. C. Birch. The intrinsic rate of natural increase of an insect population 15

T. B. Reynoldson. An ecological study of the enchytraeid worm population of sewage bacteria beds: synthesis of field and laboratory data 27

Helen Chitty. The Snowshoe Rabbit Enquiry, 1943–46 . . 39

David Lack. The significance of litter size 45

J. R. Erichsen Jones. The fauna of four streams in the 'Black Mountain' district of South Wales 51

L. S. V. Venables and U. M. Venables. A Shetland bird population: Kergord Plantations 66

A. Macfadyen. The meaning of productivity in biological systems 75

Reviews 81

Notices of publications on the Animal Ecology of the British Isles . 88

VOLUME 17, No. 1 MAY 1948

FOOD AND FEEDING RELATIONSHIPS IN A COMMUNITY OF FRESH-WATER FISHES

BY P. H. T. HARTLEY
Freshwater Biological Association, Wray Castle, Ambleside, Westmorland

(With 3 Figures in the Text)

1. INTRODUCTION

In the majority of researches upon the food of fishes attention has been fixed upon one species, and the other members of the community in which that species lives are considered chiefly as predators or as potential foods. Yet, it is generally realized that the factor of interspecific competition for supplies may be fully as rigorous as intraspecific competition in its limiting effects upon multiplication, growth and well-being. Nikolsky (1945) has named as the first problem in fish biology 'the study of the feeding habits of different species in order to understand the qualitative and quantitative connections between fishes and their food organisms. The results would be the knowledge of the dynamics of the food chains in a water body....'

Among others, Swynnerton & Worthington (1940) and Radforth (1940) in Great Britain; Alm (1917, 1921, 1922) in Sweden; Clemens, Dymond & Bigelow (1924) in Canada; Nurnberger (1930), Ewers (1933), Ewers & Boesel (1935), Boesel (1937) and Van Oosten & Deason (1937) in the United States; and Dobers (1922) and Stadel (1936) in Germany have published accounts of the foods of several species of fresh-water fish from one water. In some of these papers competition between species is not explicitly discussed, although information upon the subject is implicit. More recently, Frost (1946) has considered the food relationships of most of the species of fish in Windermere.

Between the end of 1938 and the beginning of 1941 the Freshwater Biological Association maintained a substation for the study of the biology of coarse (non-salmonid) fish at Bulbeck Mill, in the village of Barrington, Cambridgeshire. This laboratory was situated on the upper reaches of the River Cam, or Rhee, near the inflow of a small tributary, the Shepreth Brook. The fishing in a short length of the main river, and in nearly half a mile of the Shepreth Brook, was under the control of the Association. The Ouse and Cam Fishery Board kindly appointed the author, who was in charge of the investigations, an honorary bailiff, with powers to take fish by any method and at all seasons.

2. DESCRIPTION OF THE HABITAT

A map of the area from which all the fish investigated came is given in Fig. 1. The 'run' of the mill, from which the undershot wheel had been removed, is the upper limit on the main river. Below the mill the river widens into a pool about 40 ft. (13 m.) across and 6 ft. (2 m.) deep in the middle. The south bank of this pool is steep-to, with the remains of a system of revetments. The north shore is of gravelly chalk mud, steeply shelving and much grown up with *Epilobium* sp. After some 20 yd. (20 m.) the pool becomes shallower and the river thereafter flows over a bottom of gritty chalk mud in a channel 30 ft. (9 m.) wide and 2–4 ft. (*c.* 1. m.) deep. On the northern side there is a steep grass-grown bank, on the south there are grazing meadows which are under water in times of flood.

A dismantled eel-trap above the mill drains into a narrow dyke, much choked with reeds (*Phragmites communis*) and reed-mace (*Typha* sp.). This dyke curves round to join the main river at the foot of the pool below the mill.

The upper part of the Shepreth Brook runs between rows of pollard willows (*Salix* sp.) in a channel about 10 ft. (3 m.) wide, floored with clean gravel; the water is only a few inches deep. Half a mile from its junction with the river, the brook is joined by an almost stagnant creek which lies parallel to the main river among willow holts and orchards. The bottom of this creek is thickly covered with sodden leaves and fine mud. Below the mouth of this creek the brook is about 10 ft. (3 m.) wide and much overhung with willows. The water is 1–3 ft. (0·3–1 m.) deep, with a muddy bottom in the deeper stretches and a gravelly bottom in the shallows.

During the period of observation, the river rose and fell through a range of 37 in. (1 m.), the highest levels being in January and May 1939, and February and March 1940. In times of flood the north bank of the Cam and the slightly embanked south side of the Shepreth Brook were the shores of a wide, shallow lake. A gang of river cleaners cleared some of the mud

and growing weeds from the main river each summer. Shepreth Brook was cleaned out at longer intervals.

This branch of the Cam rises from chalk springs at Ashwell, and flows through agricultural country. The water is alkaline, with a pH of 8·3–8·4 and is usually turbid with chalk mud. The water of Shepreth Brook has a similar pH value, but is very clear. I am indebted to Mr R. S. A. Beauchamp for analyses of the water from the river, the brook and the dyke made at the end of April 1939 by the members of the Cambridge Zoology Department hydrobiological course (Table 1).

The records at once show the great variations in temperature conditions which fish living in small waters must endure. On several occasions the animal community of the upper Cam was subject to greater changes of temperature within one month than animals living in the English Channel would experience within a year (Harvey, 1928). The temperature variations within the day were also large. It must be emphasized that the two daily readings were not necessarily the maximum and minimum temperatures for the period, with the result that the mean daily ranges given in Table 2 may be regarded as minimal.

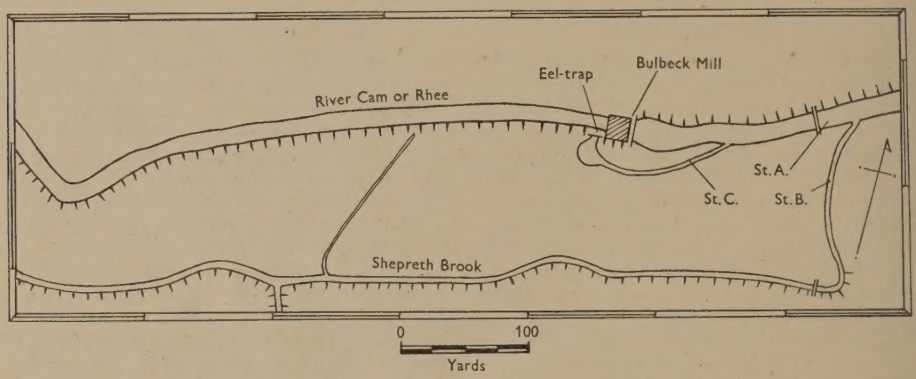


Fig. 1. River Cam and Shepreth Brook at Barrington, Cambridgeshire. The embanked shores of the river and brook are hachured.

Table 1. *Analysis of water samples from the River Cam, Shepreth Brook and Bulbeck Mill Dyke. Late April* 1939

All values expressed as p.p.m.

	River Cam St. A	Shepreth Brook St. B	Dyke St. C
O_2	15	16	16
$-CO_3''$	276	258	246
NH_3'	0·1	0·02	0·04
$-NO_2''$	0·014	0·009	0·014
$-NO_3''$	7·5	—	—
SiO_2	11·0	11·0	11·0
$-P_2O_5'''$	0·26	0·26	0·26

The temperature of the water of the main river was taken twice daily, at 09.30 and 16.30 hr. (G.M.T.), in the pool just below the mill. The water there had been well mixed by pouring over the lip of the mill run. Table 2 shows the mean morning temperature for each month, the mean daily range (that is, the mean difference between the morning and afternoon temperatures), the highest and lowest temperatures recorded during each month, and the mean air temperature at 09.30 hr.

Yet in June 1939, and May 1940, the daily range averaged more than 3·1° C. The greatest differences between morning and afternoon temperatures were 5·90 on 20 April 1939 (when the difference between the maximum and minimum air temperatures for the day was 17·40) and 5·8° on 13 August 1940 (when the mean range of air temperature was 10·5°).

Daily variation of temperature was greater in summer than in winter. There was a marked lack of regularity in the ranges of temperatures on successive days. For example, on 10 May 1939, the range of temperature for the day was 3·9°; on 11 May it was 0·3°. On 24 May 1939 the day's range of temperature was 4·5°; on 25 May it was 0·1°. The animals living in such a habitat must be strongly eurythermal.

3. MATERIAL AND METHODS

The fish examined were caught by a variety of methods—by trapping, by seine-net and hand-net, by spearing, snaring and shooting and by 'fair angling'. Except in the case of very small species and juveniles the vast majority of the specimens were secured in traps.

The traps used were made on the lobster-pot principle. Each trap (Fig. 2) consisted of a cylinder of

wire-netting lying on its side, having one end closed and the other fitted with a funnel of netting opening inwards. The first trap used was professionally built, with two compartments, each having a funnel of copper wire. All the rest of the 'fleet' were home-made, of ½ in. mesh chicken netting on a frame-work of thick galvanized wire. The entry end of each trap was fitted with a projecting hood of wire-netting, designed to increase the effective diameter of the funnel.

The 'fleet' used consisted of a dozen traps. These were dropped singly into likely places in the river and brook, with the entrance downstream. Drifting weed and rubbish settled thickly on the hoods and tops of the traps, and it is probable that the entrances appeared as gaps in obstructions in the path of the fish. It was found that certain places, especially where the water was deep and the bank steep, were profitable, and traps were kept steadily at work there.

Table 2. *Temperature conditions (in °C.) in the River Cam at Barrington, Cambridgeshire,* 1939 *and* 1940

Mean T., mean temperature for month at 09.30 hr.; Max., highest temperature recorded during month; Min., lowest temperature recorded during month; Range, mean difference between temperatures at 09.30 and 16.30 hr.

1939	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Water:												
Mean T.	5·12	5·86	6·14	9·1	11·02	13·5	15·5	15·69	13·97	8·93	8·47	6·2
Max.	8	9	8	12	14	16	17	17	17	11	10	10
Min.	0	3	4	6	7	11	13	14	9	5	5	3
Range	0·71	1·33	1·93	2·47	2·92	3·16	1·41	2·0	1·42	1·19	0·61	0·61
Air:												
Mean T.	5·5	6·0	7·02	10·9	12·91	17·42	18·25	16·6	14·83	8·28	8·6	4·55
1940												
Water:												
Mean T.	1·45	2·91	5·88	8·77	12·17	15·68	15·72	15·89	11·9	8·03	7·0	4·14
Max.	2	8	8	11	15	18	17	19	16	10	10	7
Min.	0	0	2	5	9	12	13	11	7	3	2	1
Range	0·43	0·78	1·71	2·27	3·13	3·01	2·91	2·86	3·0	2·4	0·99	0·79
Air:												
Mean T.	−1·96	2·07	5·15	9·07	13·24	17·7	15·98	15·99	13·8	7·43	6·47	3·05

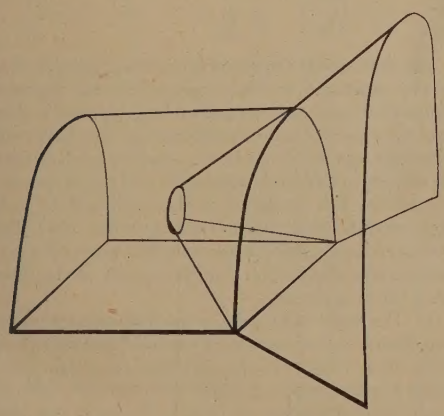


Fig. 2. Framework of fish-trap.

Fish were removed through a small door in the top of the trap. Some fish of the smaller species were caught in traps consisting of a glass jam jar with a tin funnel entrance projecting inwards. Traps of both kinds were set unbaited.

Other traps were moved about, working the less likely stretches of water. A number of fish were taken by dropping traps into 'lies' from which they had been seen to swim. Traps were lifted twice daily in winter and thrice daily in summer. Occasionally, when the water was low, traps were placed in a row across the brook and the fish were driven towards them by trawling a bag-net from the banks.

A list of the fish examined is given in Table 3. Routine investigation consisted of measurement of the length overall, and to the fork of the tail in those species with a cleft caudal fin; observation of the sex and gonad condition; and the examination of the contents of the stomach and gut. Since most of the fish were trapped, no estimates of the 'fullness' of the digestive tracts could be made. In certain species scales were collected for age determination, and the fishes were weighed.

The foods contained in the stomach and gut were identified and enumerated as exactly as their condition permitted. Unfortunately the cyprinid fishes grind their food to fragments before swallowing it and a tangled mass was found consisting of insect legs and shards and other food remnants, mixed with mud and mucus. Since the investigation of the foods of fishes from this area was but a part of a larger

programme, it was impossible to examine and count the organisms in every sample of food in detail. An arbitrary scale was therefore used—'few', 'some', 'several', 'many' and 'very many'. When compiling lists of organisms eaten, numerical values were given to these standards: 'few', 3; 'some', 5; 'several', 7; 'many', 20; and 'very many', 40. In the table of food organisms found (Table 5), the fish in which all or most of the enumerations are on this basis are marked with an asterisk. Since the values allotted are most conservative, the numbers of different organisms stated to have been eaten by these fish should be regarded as minimal.

In the autumn of 1938 there had been a severe pollution of the main river by an alkaline outflow from a cement works farther upstream, and many fish were killed thereby. The Shepreth Brook was not affected. The fishes caught in the main river were, therefore, recolonizing the depopulated area from the lower reaches, or from the tributary streams.

Table 3. *Species of fish examined*

	Total	River Cam	Shepreth Brook	Mill Dyke	No data
Pike (*Esox lucius* L.)	62	38	19	1	4
Eel (*Anguilla anguilla* (L.))	125	27	81	14	3
Gudgeon (*Gobio gobio* (L.))	391	99	273	19	—
Minnow (*Phoxinus phoxinus* (L.))	126	24	101	1	—
Dace (*Leuciscus leuciscus* (L.))	231	161	63	7	—
Roach (*Rutilus rutilus* (L.))	166	125	23	15	3
Loach (*Nemacheilus barbatula* (L.))	16	6	3	7	—
Perch (*Perca fluviatilis* L.)	8	—	8	—	—
Bullhead (*Cottus gobio* L.)	84	21	58	4	1
3-spined stickleback (*Gasterosteus aculeatus* L.)	227	151	34	42	—
Brown trout (*Salmo trutta* L.)	30	4	26	—	—

4. FOOD AND FEEDING RELATIONSHIPS OF THE FISHES

The foods of the fish were listed in two ways: first, in order to find out the general feeding habits of each species; and secondly, to discover the organisms on which each species had fed. In the investigation of feeding habits, the foods were divided into a number of categories—fish, molluscs, insects, Crustacea, vascular plants and filamentous algae, diatoms, etc.—and lists were made of the number of fish of each species in which foods of any of these categories were found. In this first analysis no account was taken of the relative abundance of the different foods: one insect larva or a hundred larvae were alike listed as one occurrence of insect food. The occurrences of food of the different categories in each species of fish are shown in Table 4, both in actual numbers and in expression of these numbers as percentages of the total. The percentage occurrence of foods of the different categories are also shown in Fig. 3.

After this first analysis had been made, lists were prepared of the recognizable organisms found in each fish, showing both the number of fish in which each organism occurred and the number of this organism found in all the fish of each species investigated. These lists are shown in Table 5. Tables 4 and 5 form the basis of discussion of the food and feeding habits of the fish and the possibilities of competition between one species and another.

On the basis of feeding habits, the fish of the Barrington district may be divided into four groups:

(1) Specialist predators upon a single prey—the pike.

(2) Fish taking a wide variety of foods—the eel and the brown trout.

(3) Fish taking a diet in which insects and plants predominate—roach, dace and minnow.

(4) Fish eating a diet in which insects and crustaceans predominate—gudgeon, bullhead and stickleback.

Perch and loach were not classified; the latter species probably belongs to the fourth group.

The dietaries of the members of these groups must now be compared, in order to find out what degree of competition may exist within each group, and to what extent the members of the different groups may compete with one another. In the absence of data upon the density of the food organisms, and the proportion removed by fish predation in the course of the year, 'competition' here means nothing more exact than 'taking an appreciable proportion of a common food', without any implication that the supply of that food was a limiting factor.

(1) The fish-eating pike is the end-point of many food chains in fresh waters. Trout and eels eat several of the same fishes as pike, and the insect and crustacean foods taken by juvenile pike are also eaten by a number of other species of fish. An adult pike may eat the actual fish which competed with it in its youth. Pike are remarkable as the only fresh-water fish eating sticklebacks in any numbers (14 occurrences and 20 individual preys).

(2) Of the fish of the second group, brown trout and eels, which show no specialization of feeding habits, brown trout are the more remarkable for the

Table 4. *Food of fish in the River Cam and Shepreth Brook*, 1939–41

The number of occurrences (=of fish containing) of food of each category is shown: and in each species of fish, the occurrences of food of each category are expressed as percentages of the total occurrence of foods (=total fish containing foods) of all categories.

	Mammals		Amphibia		Fish		Mollusca		Insecta		Myriapoda		Arachnida		Crustacea		Oligochaeta		Vascular plants and filamentous algae		Diatoms	
	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%
Pike	—	—	—	—	45	**85**	—	—	5	**9**	—	—	—	—	3	**6**	—	—	—	—	—	—
Eel	1	**1**	—	—	28	**19**	7	**5**	36	**24**	—	—	—	—	66	**44**	2	**1**	8	**5**	—	—
Gudgeon	—	—	—	—	—	—	60	**12**	281	**57**	—	—	1	/	119	**24**	1	/	27	**6**	2	/
Minnow	—	—	—	—	—	—	—	—	65	**43**	1	**1**	5	**3**	14	**9**	—	—	32	**21**	34	**23**
Dace	—	—	—	—	—	—	22	**9**	135	**53**	—	—	—	—	16	**6**	—	—	56	**22**	27	**10**
Roach	—	—	—	—	—	—	35	**19**	66	**36**	—	—	1	**1**	13	**7**	—	—	55	**30**	12	**7**
Loach	—	—	—	—	—	—	—	—	13	(65)	—	—	—	—	7	(35)	—	—	—	—	—	—
Perch	—	—	—	—	1	(10)	—	—	3	(30)	—	—	—	—	6	(60)	—	—	—	—	—	—
Bullhead	—	—	—	—	—	—	1	**1**	58	**58**	—	—	—	—	39	**39**	3	**3**	—	—	—	—
3-spined stickleback	—	—	—	—	—	—	7	**2**	150	**51**	—	—	1	**1**	69	**24**	1	**1**	42	**14**	23	**8**
Brown trout	1	**1·5**	1	**1·5**	8	**13**	4	**7**	29	**48**	—	—	1	**1·5**	13	**21**	2	**3**	2	**3**	1	**1·5**

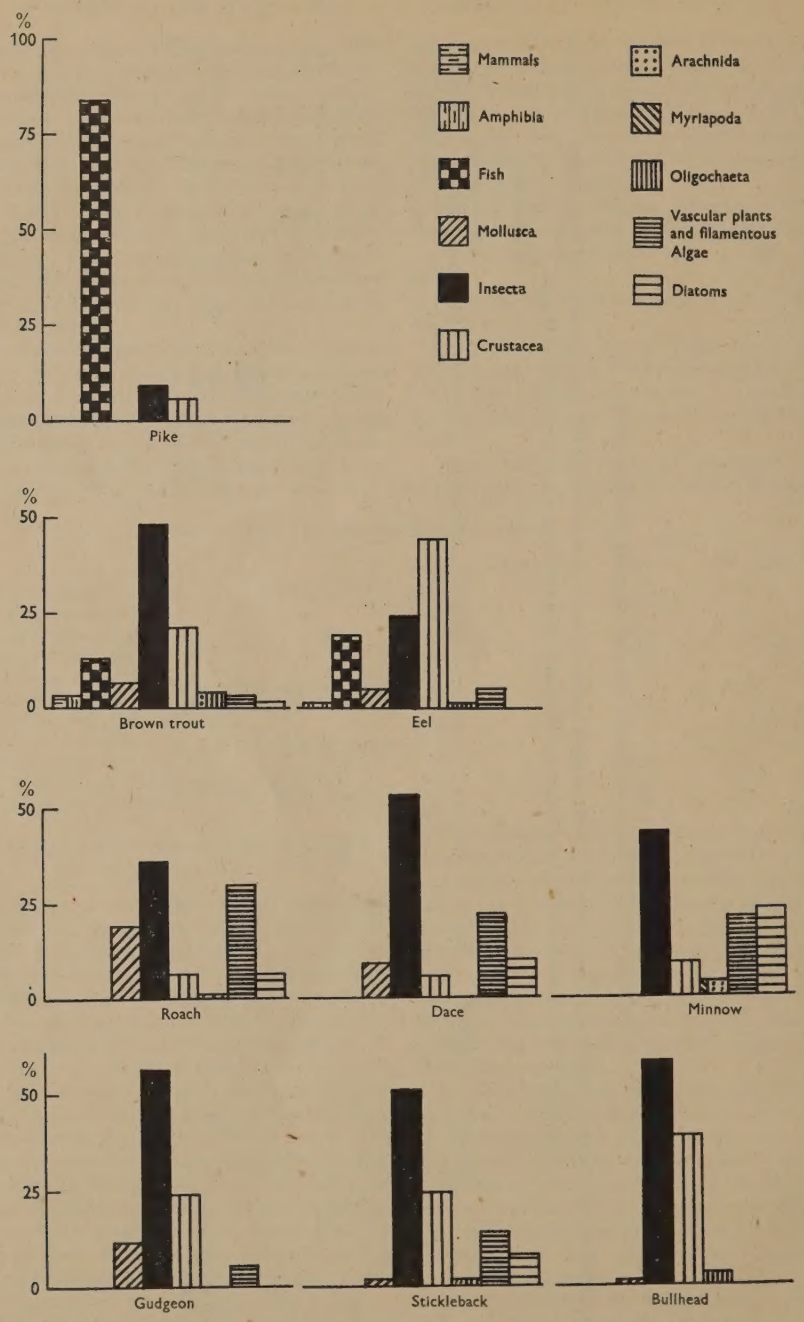


Fig. 3. Food of fish in the River Cam and Shepreth Brook at Barrington, Cambridgeshire, in 1939–41. In each species of fish the occurrences of different foods are expressed as percentages of the total occurrences of foods of all kinds.

Table 5. *Food of fish in the River Cam and Shepreth Brook*, 1939–41

The number of fish in which each food was found is shown, and (when the numerical method of expression is suitable) in italics—the total number of each food organism.

	Pike		Eel		*Gudgeon		*Minnow		*Dace		*Roach		Loach		Perch		Bullhead		*3-spined stickle-back		Brown trout	
	Occ.	No.	Occ.	No.	Occ.	No.	Occ.	No.	Occ.	No.	Occ.	No.	Occ.	No.	Occ.	No.	Occ.	No.	Occ.	No.	Occ.	No.
Mammals																						
Apodemus sylvaticus (L.)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	*1*
Microtus sp.	—	—	1	*1*	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Amphibia																						
Rana temporaria L.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	*1*
Fish																						
Anguilla anguilla (L.)	1	*1*	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Phoxinus phoxinus (L.)	3	*3*	2	*5*	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Gobio gobio (L.)	7	*7*	3	*3*	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	*3*
Rutilus rutilus (L.)	2	*2*	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Nemacheilus barbatula (L.)	3	*3*	2	*2*	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Cottus gobio L.	3	*3*	2	*2*	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Gasterosteus aculeatus L.	14	*20*	2	*2*	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	*1*
Cyclostomata																						
Lampetra fluviatilis (L.)	—	—	7	*12*	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Mollusca:																						
Lamellibranchiata																						
Sphaerium sp.	—	—	—	—	1	*1*	—	—	—	—	—	—	—	—	—	—	—	—	1	*2*	—	—
Gastropoda																						
Hydrobia jenkinsi Smith	—	—	1	*1*	10	*189*	—	—	6	*107*	11	*107*	—	—	—	—	—	—	1	*1*	3	*43*
Ancylus fluviatilis (Müll.)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	*1*
Limnaea pereger (Müll.) and sp.	—	—	4	*27*	—	—	—	—	1	*1*	—	—	—	—	—	—	—	—	1	*4*	1	*1*
Planorbis sp.	—	—	1	*1*	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Arachnida																						
Aranaeid indet.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	*2*
Limnocarid indet.	—	—	—	—	—	—	—	—	—	—	1	*10*	—	—	—	—	—	—	—	—	—	—
Hygrobatid indet.	—	—	—	—	—	—	1	*1*	—	—	1	*1*	—	—	—	—	—	—	—	—	—	—
Hydracarinids indet.	—	—	—	—	1	*1*	3	*3*	—	—	—	—	—	—	—	—	—	—	1	*1*	—	—
Myriapoda																						
Myriapoda indet.	—	—	—	—	—	—	1	*3*	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Insecta:																						
Ephemeroptera																						
Ephemera sp., adult	1	*1*	—	—	—	—	—	—	—	—	—	—	1	*1*	—	—	—	—	—	—	3	*6*
Ephemera vulgata L. and sp., nymph	1	*1*	3	*7*	—	—	1	*1*	1	*7*	—	—	—	—	—	—	2	*2*	—	—	3	*4*
Leptophlebia cincta (Retzius) and sp., nymph	—	—	1	*4*	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	*3*
Baetis sp., nymph	1	*1*	2	*8*	8	*87*	1	*2*	3	*5*	—	—	1	*1*	—	—	1	*1*	11	*22*	1	*1*
Centroptilum sp., nymph	1	*1*	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	*1*	—	—
Ephemeropteran indet., adult	—	—	—	—	—	—	—	—	1	*20*	—	—	—	—	—	—	—	—	—	—	1	*1*
Ephemeropteran indet., nymph	—	—	11	*48*	24	*82*	2	*3*	6	*30*	3	*23*	2	*4*	—	—	6	*8*	9	*11*	3	*10*

Table 5 (*continued*)

Insecta (*continued*):	Pike		Eel		Gudgeon		Minnow		Dace		Roach		Loach		Perch		Bullhead		3-spined stickle-back		Brown trout	
	Occ.	No.	Occ.	No.	Occ.	No.	Occ.	No.	Occ.	No.	Occ.	No.	Occ.	No.	Occ.	No.	Occ.	No.	Occ.	No.	Occ.	No.
Hemiptera																						
Corixa striata (L.)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	1
Corixids indet., adult	—	—	—	—	—	—	1	1	4	5	1	1	—	—	—	—	—	—	2	3	4	8
Corixids indet., nymph	—	—	—	—	—	—	—	—	1	1	—	—	—	—	—	—	—	—	1	1	—	—
Megaloptera																						
Sialis lutaria (L.), larva	—	—	3	3	15	19	—	—	4	8	3	5	1	1	2	2	7	9	1	1	4	4
Trichoptera																						
Rhyacophila dorsalis (Curt.), larva	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	2
Hydroptila sp., larva	—	—	—	—	—	—	—	—	1	1	1	1	—	—	—	—	—	—	1	1	1	3
Polycentropus sp., larva	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	2
Hydropsyche sp., larva	—	—	2	2	2	2	—	—	3	5	—	—	—	—	—	—	4	10	—	—	1	1
Phryganea sp., larva	—	—	—	—	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Leptocerus sp., larva	—	—	—	—	2	5	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	2
Molanna angustata Curt. and sp., larva	—	—	—	—	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	3
Glyphotaelius sp., larva	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	1	—	—	—	—
Limnophilus sp., larva	—	—	1	1	4	7	—	—	—	—	—	—	2	3	—	—	1	1	—	—	—	—
Anabolia nervosa Curt., larva	—	—	1	1	—	—	—	—	18	37	2	5	—	—	—	—	1	1	—	—	4	5
Stenophylax sp., larva	—	—	—	—	2	4	—	—	11	24	—	—	—	—	—	—	2	2	—	—	2	2
Halesus sp., larva	—	—	—	—	—	—	—	—	1	2	—	—	—	—	—	—	—	—	—	—	1	7
Trichopteran indet., adult	—	—	—	—	—	—	—	—	1	2	—	—	—	—	—	—	—	—	—	—	2	22
Trichopteran indet., larva	—	—	2	4	12	15	2	3	35	87	3	6	1	2	—	—	2	2	1	1	10	35
Lepidoptera																						
Moths indet., adult	—	—	—	—	—	—	—	—	1	7	—	—	—	—	—	—	—	—	—	—	1	2
Caterpillars indet.	—	—	3	4	—	—	—	—	3	3	1	1	—	—	—	—	—	—	—	—	1	1
Coleoptera																						
Dytiscus marginalis L. and sp., adult	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	3	3
D. marginalis L. and sp., larva	—	—	1	1	4	5	—	—	1	1	2	3	—	—	1	1	1	1	—	—	4	6
Hydroporus sp., adult	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	1
Hygrobia hermanni (Fab.), adult	—	—	—	—	—	—	—	—	1	1	—	—	—	—	—	—	—	—	—	—	—	—
Dryops sp., larva	—	—	—	—	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Gyrinus sp., adult	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	1
Helodes sp., larva	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	1	—	—	—	—
Coleopteran indet., adult	—	—	2	2	8	11	2	3	18	31	2	6	—	—	—	—	—	—	—	—	9	95
Coleopteran indet., larvae	—	—	—	—	1	1	—	—	—	—	—	—	—	—	—	—	1	1	—	—	—	—

Hymenoptera																						
Chalcidoids indet., adult	—	—	—	—	—	—	—	—	3	10	1	2	—	—	—	—	—	—	1	1	—	—
Hymenopterans indet., adult	—	—	—	—	1	1	2	3	3	6	—	—	—	—	—	—	—	—	—	—	3	3
Diptera																						
Tipula sp., larva	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	1	—	—	—	—
Dicranota sp., larva	—	—	—	—	6	13	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Tipulid indet., larva	—	—	1	1	2	4	—	—	—	—	1	1	—	—	—	—	4	8	—	—	—	—
Simulium sp., larva	—	—	7	37	35	376	2	4	19	93	10	70	4	25	—	—	4	5	4	6	1	3
Simulium sp., pupa	—	—	—	—	1	1	—	—	—	—	2	6	—	—	—	—	—	—	—	—	—	—
Tanypus sp., larva	—	—	—	—	2	28	—	—	—	—	1	7	1	2	—	—	—	—	2	25	—	—
Corynoneura sp., larva	—	—	—	—	—	—	—	—	—	—	1	2	—	—	—	—	1	1	—	—	—	—
Forcipomyia sp., larva	—	—	—	—	24	110	1	2	—	—	—	—	1	2	—	—	1	1	1	2	—	—
Chironomus sp. and chironomid indet., larva	2	3	3	4	212	1565	33	115	28	94	22	55	6	16	—	—	16	68	67	285	—	—
Chironomid indet., pupa	—	—	1	1	3	23	5	9	2	4	1	5	—	—	—	—	2	2	10	21	—	—
Culicid indet., pupa	—	—	—	—	—	—	1	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Tabanid indet., larva	1	1	—	—	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Anthomyiid indet., larva	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	1	—	—	—	—
Dipterans indet., adult	—	—	—	—	2	7	4	7	4	8	4	8	—	—	—	—	—	—	—	—	10	80
Crustacea																						
Potamobius pallipes Lereboullet (=*Astacus fluviatilis* L.)	1	1	33	43	—	—	4	4	1	1	—	—	—	—	—	—	3	3	—	—	3	3
Gammarus pulex (de Geer)	2	6	39	225	71	281	5	5	13	67	14	34	3	17	6	13	34	40	2	2	10	24
Asellus aquaticus Leach and sp.	1	1	2	2	—	—	—	—	1	1	—	—	—	—	—	—	3	8	1	1	1	1
Oniscus sp.	—	—	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Chydorus sp.	—	—	—	—	29	135	2	8	—	—	—	—	3	5	—	—	—	—	14	35	—	—
Cyclops sp.	—	—	—	—	—	—	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Copepoda indet.	—	—	—	—	35	145	2	5	—	—	2	8	1	2	—	—	1	1	54	215	—	—
Ostracoda indet.	—	—	1	1	15	53	—	—	—	—	—	—	—	—	—	—	—	—	8	24	—	—
Oligochaeta																						
Earthworm indet.	—	—	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	1
Oligochaete indet.	—	—	—	—	2	3	—	—	—	—	—	—	—	—	—	—	—	—	1	2	—	—
Hirudinea																						
Herpobdella octoculata L. and sp.	—	—	1	1	—	—	—	—	—	—	—	—	—	—	—	—	3	3	—	—	—	—
Plants																						
Sparganium sp.	—	—	—	—	—	—	—	—	7	—	2	—	—	—	—	—	—	—	—	—	—	—
Ulothrix sp.	—	—	—	—	—	—	—	—	4	—	2	—	—	—	—	—	—	—	—	—	1	—
Cladophora sp.	—	—	—	—	—	—	—	—	10	—	10	—	—	—	—	—	—	—	—	—	—	—
Spirogyra sp.	—	—	—	—	—	—	—	—	8	—	1	—	—	—	—	—	—	—	—	—	—	—
Vaucheria sp.	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	1	—

wide variety of their diet. Forty-nine recognizable genera or species of prey were found in 30 fish, an average of 1·63 different preys per trout, as compared with an average of 0·26 different preys per eel (33 recognizable on 125 fish). The high proportion of the number of recognizable organisms to number of fish examined which is found in the trout is not due to difference in degrees of mastication, for both trout and eels tend to bolt their food whole. Larval Trichoptera, occurring in 25 out of 30 fish (84 %), were the insect food most often eaten by brown trout, 62 individuals belonging to nine genera being found. Adult beetles, occurring in 13 out of 30 fish (43 %) and adult Diptera in 10 fish (33 %) were next in importance, with some nymphal and adult Ephemeroptera, larvae of beetles and *Sialis* sp. and adult corixids. Trout differed markedly from all other insect-eating fish in these waters in that chironomid larvae formed no part of their diet, and that larvae of *Simulium* sp. were found but once (three larvae in one fish). *Gammarus pulex* occurred in 10 fish (33 % occurrence) and *Astacus fluviatilis* in 3 (10 %). Three trout had eaten *Hydrobia jenkinsi*.

On a basis of occurrence, insects made up 48 % of the diet of brown trout, and Crustacea 21 %. In the eel these proportions were almost exactly reversed, insects, contributing 24 % of the diet and Crustacea 44 %. Ephemeropteran nymphs were the insect food most often taken by eels, 67 individuals being found in 17 eels out of 125 (13·6 % occurrence); 37 larvae of *Simulium* sp. were found in 7 eels (5·6 % occurrence) and trichopteran larvae in 6 (4·8 %). *Gammarus pulex* was the chief crustacean food of eels as well as of trout, being found in 39 fish out of the 125 (31 %), but eels contained more than twice as many gammarids per stomach, 5·8 per fish, as compared with 2·4 in trout. Eels took many *Astacus fluviatilis*, 43 specimens being found in 33 fish (26 %).

(3) In the third group, in which insects and plants are the most important items in the dietary, there is some competition between the three members—roach, dace and minnow—but the proportions in which the more numerously occurring foods were eaten showed considerable differences.

Chironomid larvae occurred in 34 minnows out of 129 examined (26·5 % occurrence), in 24 roach out of 163 (14·5 %) and in 28 dace out of 231 (12 %). The larvae of *Simulium* sp. were found in 19 dace (8 %), in 10 roach (6 %) and in 2 minnows (1·5 %). Trichopteran larvae were the insect food most often taken by dace, 166 larvae belonging to at least five genera being found in 69 fish (30 % occurrence), but only 6 roach (3·5 %) and no minnows contained this food. Nineteen dace (8 %) contained adult beetles, but these insects were found in only 2 roach and 2 minnows. Ephemeropteran nymphs were found in 10 dace (4 %), in 3 roach (2 %) and in 4 minnows (3 %).

The plant foods eaten by these three species consist largely of filamentous algae. In the summer months the production of such algal food is enormous, great mats of 'flannel weed' drifting down the river and stranding in the shallows. In the presence of such a superabundance of plant food it is not to be believed that there can exist any pressure upon the supply for at least half the year, and even in winter long strands of algae are to be found growing on piles and stones. Diatoms are a food of young roach and dace (Hartley, 1947), but they make a substantial contribution to the diet of minnows of all sizes.

Of the crustaceans eaten *Gammarus pulex* occurred most frequently, 34 specimens being found in 14 roach (8·5 %), 67 in 13 dace (5·5 %) and one in each of 5 minnows (4 %). Four minnows had each eaten one very small *Astacus fluviatilis*.

Hydrobia jenkinsi was found in 11 roach (7 %) and in 6 dace (2·5 %).

(4) In the fourth group, in which the food is composed of insects and crustaceans, there is considerable competition between all three members for insect foods, between gudgeon and bullhead for the larger Crustacea, and between gudgeon and stickleback for the smaller.

In gudgeon and stickleback, chironomid larvae were by far the most important food; they occurred in 238 gudgeon out of 391 (61 %) and in 95 sticklebacks out of 227 (42 %). In loach, chironomid larvae were found in 8 (50 %) of the 16 fish examined, and in the bullhead, which took a higher proportion of Crustacea than the other members of the group, chironomid larvae formed the insect food most frequently occurring, being found in 18 fish out of 84 (21·5 %). Of other insect foods, ephemeropteran nymphs were found in 9 bullheads (11 %), 21 sticklebacks (9 %), 32 gudgeon (8 %) and in 4 out of 16 loach. Trichopteran larvae had been eaten by 11 bullheads (13 %), 24 gudgeon (6 %), 3 loach and only 3 sticklebacks (1 %). Gudgeon differed from the other fish of the group in taking many larvae of *Simulium* sp. These were found in 35 fish (9 %).

Gammarus pulex was the food most often eaten by bullheads, being found in 34 fish (40·5 %); 71 gudgeon (18 %) had eaten *Gammarus* and so had 3 loach. The average number of *G. pulex* found in gudgeon was 4 (281 specimens in 71 fish), but in bullheads the average consumption was only a little over 1·1 (40 specimens in 34 fish). The 3 loach which had eaten this food contained 17 between them.

Of the smaller Crustacea, Copepoda were an important food of sticklebacks, being found in 54 fish (24 %). Thirty-four gudgeon (8·5 %) and 1 bullhead had eaten copepods. Twenty-nine gudgeon (7·5 %) and 14 sticklebacks (6 %) had eaten *Chydorus* sp., and 3 loach contained Cladocera of this genus.

The fishes of the community have been divided

into four groups, on a somewhat arbitrary basis of differences of general feeding habits: but it is immediately obvious that competition for certain foods is not confined within group limits. Table 6 shows the frequency of occurrence of certain foods, expressed as a percentage of the fish of each species examined in which these foods were found. This table emphasizes both competition within groups and competition between members of different groups. For example, chironomid larvae are an important food of all members of groups 3 and 4 (in which a high consumption of insect food is the common feature of the dietaries). Trichopteran larvae are the most frequently occurring insect foods of both brown trout and dace, and only these two species consume any quantity of adult beetles. The fact that brown trout take no dipteran larvae is a distinction between their insect diets. There is a certain similarity between the diets of the small bullheads and the relatively large brown trout and eels. Of 21 identifiable foods eaten by bullheads, 9 had also been eaten by both brown trout and eel, 4 by eels only, 1 by brown trout only.

The activities of the fish fauna do not complete the tale of vertebrate predation upon the population of the river. Otters (*Lutra lutra*), herons (*Ardea cinerea*), kingfishers (*Alcedo atthis*) and little grebes (*Podiceps ruficollis*) all visited the area. In addition to their direct toll, a number of aquatic birds competed with the fishes for invertebrate foods. The stomach contents of 10 moorhens (*Gallinula chloropus*), 1 tufted duck (*Aythya fuligula*) and 2 common snipe (*Capella gallinago*) from this stretch of the Cam were examined. The food of these birds is shown in Table 7.

Table 6. *Animal foods found most frequently in fish from the River Cam and Shepreth Brook in* 1939–41

In each species of fish, the number of fish in which each food occurred is expressed as a percentage of the total number of fish examined.

	Fish	Ephemeropteran nymphs	Trichopteran larvae	Adult beetles	Larvae of *Simulium* sp.	Chironomid larvae	*Potamobius pallipes* (=*Astacus fluviatilis*)	*Gammarus pulex*	Copepoda	*Chydorus* sp.
Pike	73	—	—	—	—	—	—	—	—	—
Brown trout	26·5	26·5	84	43	—	—	10	33	—	—
Eel	22	13·6	—	—	5·6	—	26	31	—	—
Roach	—	—	—	—	6	14·5	—	8·5	—	—
Dace	—	—	30	8	8	12	—	5·5	—	—
Minnow	—	—	—	—	—	26·5	—	—	—	—
Gudgeon	—	8	6	—	9	61	—	18	8·5	7·5
Stickleback	—	9	—	—	—	42	—	—	24	6
Bullhead	—	11	13	—	—	21·5	—	40·5	—	—

Table 7. *Food of aquatic birds, River Cam and Shepreth Brook,* 1939–41

Of the 10 moorhens, 5 were adult and 5 juveniles in down.

	Tufted duck		Common snipe		Moorhen	
	Occ.	No.	Occ.	No.	Occ.	No.
Hydrobia jenkinsi Smith	—	—	1	*1*	2	*3*
Ephemeropteran indet., nymph	—	—	—	—	1	*1*
Sialis sp., larva	1	*2*	1	*8*	—	—
Hydropsyche sp., larva	1	*4*	—	—	—	—
Stenophylax sp., larva	1	*1*	—	—	—	—
Coleopteran indet., adult	—	—	—	—	3	*5*
Dytiscus sp., larva	1	*2*	—	—	—	—
Tipula sp., larva	—	—	2	*18*	—	—
Simulium sp., larva	—	—	—	—	1	*1*
Gammarus pulex (de Geer)	1	*16*	—	—	—	—
Elodea sp.	—	—	—	—	1	/
Sparganium sp.	—	—	—	—	1	/
Carex sp. (seeds)	—	—	—	—	1	(*25*)
Cladophora sp.	—	—	—	—	1	/

Three 'links' of a few food chains have been established by direct observation, and these are shown in Table 8.

Percival & Whitehead (1929) recorded that 'the carnivorous species do not form more than 10% of the total (invertebrate) fauna of a given type of substratum', and Slack (1936) has shown the predominance of an herbivorous feeding habit among trichopteran larvae. Feeding largely upon herbivorous animals, the members of the fish fauna stand in a qualitatively simple relationship to the invertebrate community. Usually there is but one connecting link between plant material and fish, and in group 3 (the fishes of partially vegetarian habit), this link is often omitted. It would be easy to construct many more food chains by deduction, but they would serve only to emphasize the predominance of the simple system: plant—invertebrate herbivore—vertebrate predator.

Table 8. *Food chains in the River Cam and Shepreth Brook*, 1939–41

(1) 31 Mar. 1939	*Spirogyra* sp.	Gudgeon	Pike	—
(2) 27 May 1939	Plant fragments	Chironomid larvae	Stickleback	Pike
(3) 19 July 1939	—	Nymph of *Ephemera* sp., larvae of *Simulium* sp.	Gudgeon	Pike
(4) 27 July 1939	Plant fragments	Stickleback	Pike	—
(5) 7 Oct. 1939	—	Nymphs of *Baetis* sp., larvae of *Simulium* sp.	Minnow	Pike
(6) 1 Dec. 1939	—	Larvae of trichopteran, 2	Stickleback	Pike
(7) 14 Mar. 1940	*Meridion circulare* and *Synedra* sp., many Naviculid indet., 1	Larvae of *Simulium* sp.	Bullhead	—
(8) 9 Apr. 1940	—	Larvae of trichopteran	Stickleback	Pike
(9) 2 June 1940	—	Nymph of *Ephemera* sp. nymph of ephemeropteran, 2, larvae of *Limnophilus* sp., 2, chironomid larvae, *Gammarus pulex*	Loach	Eel
(10) 18 July 1940	Plant fragments and diatom frustules	Larvae of *Simulium* sp.	Dace	—
	Plant fragments	Larvae of *Simulium* sp.	Dace	—
	Plant fragments and diatom frustules	Larvae of *Simulium* sp.	Dace	—
(11) 30 July 1940	—	Nymph of *Baetis* sp., 1, chironomid larva, 1	Bullhead	Pike
(12) 1 Aug. 1940	*Coscinodiscus* sp. and naviculid diatoms	Larva of *Simulium* sp.	Gudgeon	—
(13) 2 June 1941	*Synedra* sp. and naviculid diatoms	Larva of *Simulium* sp.	Trout	—

5. DISCUSSION

When the feeding habits and relationships of the fishes living in the waters at Barrington have been surveyed, it is possible to make three generalizations about them. First, between no two species is there a true identity of feeding habit. The nearest approach to a common dietary is in gudgeon and stickleback. In these two species insects contributed 57 and 51% of the total occurrences of food, and of insect food three groups, ephemeropteran nymphs and larvae of *Simulium* sp. and of chironomids contributed 82 and 89% respectively on a basis of occurrence, and 95 and 93% on a basis of numbers. Yet in the foods of these two species there are contrasts quite as marked as the similarities: *Gammarus pulex* contributed 48% of the crustacean foods found in gudgeon, and only 1·3% in the stickleback. 12% of the gudgeon food was molluscs and only 2% of the sticklebacks. In gudgeon only 6% of the occurrences of food was of plant origin, but in sticklebacks vascular plants and algae contributed 14% of the food, and diatoms 8%. In the same way it has been shown that there is a marked similarity between the insect foods of trout and dace, and wide dissimilarity in the constitution of the rest of their diet.

Secondly, it may be concluded that, with the exception of the fish-eating pike, there is a great degree of general competition between all the fish of

the community. While no instance has been found of two species occupying one ecological niche, as bream (*Abramis brama* (L.)) and white bream (*Blicca bjoernka* (L.)) appear to do in some East Anglian waters (Hartley, 1947), none of the species present have clearly defined individual roles to play. Here is no orderly hierarchy of specialists, each fulfilling its part, but rather a loosely organized assemblage in which the members are distinguished by no more than the varying proportions in which they draw upon the constituents of a common stock. It has been shown elsewhere (Hartley, 1940) that most of the 'coarse' fishes show considerable flexibility of feeding behaviour, and it is by no means certain that the balance of relationships revealed in the period 1939–41 will be maintained unaltered. In the absence of any evidence of the actual degree of pressure upon the food supplies it is impossible to say to what extent 'competition' between different species is a limiting factor upon growth and numbers; and the ability of most of the members of the community to live and thrive upon a wide variety of foods will make the effects of the failure of any one source of supply less disturbing of the general balance than they would be in a community in which ecological niches were more clearly defined.

Thirdly, it must be concluded that the organization of this animal community is qualitatively straightforward. There are but two or three steps between the supply of plant material and the end-point of the food chain. This is not to suggest that the ecological relationships within a 'small river' community are entirely simple, but complexities will be quantitative rather than qualitative. It has been shown that the differences between the food requirements of one species and another lie in the different inroads which they make upon the components of a common stock. As the supply of one food becomes more abundant, and of another scarce, so the balance of competition between one species and another will be altered. Though no complete identities of diet have been found, the degree of general competition is such that few of the members of the fish fauna will be wholly unaffected by an enforced change in the diet of some other species.

SUMMARY

1. A short stretch of the upper reaches of the River Cam and one of its tributaries, the Shepreth Brook, contained a community of eleven species of fish. The area is defined and briefly described.

2. An investigation was made of the food of the members of the fish community, and of a few aquatic birds from the same area. It is shown that, on a basis of food, the fish may be divided into four groups:

(*a*) Specialist predators upon a single prey. One species.

(*b*) Fish taking a wide variety of foods. Two species.

(*c*) Fish taking a diet in which insects and plants predominate. Three species.

(*d*) Fish taking a diet in which insects and crustaceans predominate. Four species.

3. It is shown that between no two species is there complete identity of feeding habit, but that there is much general competition between all the fish of the community for certain staple foods.

REFERENCES

Alm, G. (1917). 'Undersökningar rörande Hjalmarens Naturforhallenden och Fiske.' Medd. LantbruksStyr. Stockh. No. 204 (No. 2 ar 1917): 1–111.

Alm, G. (1921). 'Klotentjärnarna.' Medd. Lantbruks-Styr. Stockh. No. 232 (No. 3 ar 1921): 119–44.

Alm, G. (1922). 'Botten faunan och Fiskens Biologici Yxtasjön.' Medd. LantbruksStyr. Stockh. No. 236 (No. 2 ar 1922): 1–186.

Boesel, W. M. (1937). 'The food of nine species of fish from the western end of Lake Erie.' Trans. Amer. Fish. Soc.: 215–23.

Clemens, W. A., Dymond, J. R. & Bigelow, N. K. (1924). 'Food studies of Lake Nipigon fishes.' Univ. Toronto Stud., Biol. Ser. No. 25: 103–65.

Dobers, E. (1922). 'Nahrungsuntersuchungen bei Wildfischen.' Z. Fisch. 21: 151–205.

Ewers, L. A. (1933). 'Summary report of Crustacea used as food by the fishes of the western end of Lake Erie.' Trans. Amer. Fish. Soc.: 379–90.

Ewers, L. A. & Boesel, W. M. (1935). 'The food of some Buckeye Lake fishes.' Trans. Amer. Fish. Soc.: 57–70.

Frost, W. E. (1946). 'On the food relationships of fish in Windermere.' 13th Biol. Jaarb., Dodonea.: 216–31.

Hartley, P. H. T. (1940). 'The food of coarse fish: being the interim report on the coarse fish investigation.' Freshw. Biol. Assoc. Sci. Publ. No. 3: 1–33.

Hartley, P. H. T. (1947). 'The natural history of some British freshwater fishes.' Proc. Zool. Soc. Lond. 117: 129–206.

Harvey, H. W. (1928). 'The biological chemistry and physics of sea water.' Cambridge.

Nikolsky, G. (1945). 'The principal problems of the modern ichthyology.' Bull. Soc. Nat. Moscou, Sect. Biol. 5–6: 1–13.

Nurnberger, P. K. (1930). 'The plant and animal food of the fishes of Big Sandy Lake.' Trans. Amer. Fish. Soc.: 253–9.

Percival, E. & Whitehead, H. (1929). 'A quantitative study of the fauna of some types of stream-bed,' J. Ecol. 17: 282–314.

Radforth, I. (1940). 'The food of the grayling (*Thymallus thymallus*), flounder (*Platichthys flesus*), roach (*Rutilus rutilus*) and gudgeon (*Gobio fluviatilis*), with special reference to the Tweed watershed.' J. Anim. Ecol. 9: 302–18.

Slack, H. D. (1936). 'The food of caddis fly (Trichoptera) larvae.' J. Anim. Ecol. 5: 105–15.

Stadel, O. (1936). 'Nahrungsuntersuchungen an Elbfischen.' Z. Fisch. 34: 45–61.

Swynnerton, G. H. & Worthington, E. B. (1940). 'Notes on the food of fish in Haweswater (Westmorland).' J. Anim. Ecol. 9: 183–7.

Van Oosten, J. & Deason, H. J. (1937). 'The food of the lake trout (*Cristivomer namaycush*) and of the lawyer (*Lota maculosa*) of Lake Michigan.' Trans. Amer. Fish. Soc.: 155–77.

THE INTRINSIC RATE OF NATURAL INCREASE OF AN INSECT POPULATION

By L. C. BIRCH*, *Zoology Department, University of Sydney*

CONTENTS

	PAGE
1. Introduction	15
2. Biological significance of the intrinsic rate of natural increase	16
3. Calculation of the intrinsic rate of natural increase	17
(*a*) Experimental data required	17
(*b*) The net reproduction rate	18
(*c*) The mean length of a generation	18
(*d*) The calculation of '*r*'	19
4. The stable age distribution	20
5. The instantaneous birth-rate and death-rate	21
6. The effect of temperature on '*r*'	21
7. Discussion	22
8. Summary	25
9. Acknowledgements	25
References	26

1. INTRODUCTION

The intrinsic rate of increase is a basic parameter which an ecologist may wish to establish for an insect population. We define it as the rate of increase per head under specified physical conditions, in an unlimited environment where the effects of increasing density do not need to be considered. The growth of such a population is by definition exponential. Many authors, including Malthus and Darwin, have been concerned with this and related concepts, but there has been no general agreement in recent times on definitions. Chapman (1931) referred to it as 'biotic potential', and although he does state in one place that biotic potential should in some way combine fecundity rate, sex ratio and survival rate, he never precisely defined this expression. Stanley (1946) discussed a somewhat similar concept which he called the 'environmental index'. This gives a measure of the relative suitability of different environments, but it does not give the actual rate of increase of the insect under these different conditions. An index for the possible rate of increase under different physical conditions would at the same time provide a measure of the relative suitability of different environments. Birch (1945*c*) attempted to provide this in an index combining the total number of eggs laid, the survival rate of immature stages, the rate of development and the sex ratio. This was done when the author was unaware of the relevance of cognate studies in human demography. A sounder approach to insect populations based on demographic procedures is now suggested in this paper. The development of this branch of population mathematics is principally due to A. J. Lotka. From the point of view of the biologist, convenient summaries of his fundamental contributions to this subject will be found in Lotka (1925, Chapter 9; 1939 and 1945). A numerical example of the application of Lotka's methods in the case of a human population will be found in Dublin & Lotka (1925). The parameter which Lotka has developed for human populations, and which he has variously called the 'true' or 'inherent' or 'intrinsic' rate of natural increase, has obvious application to populations of animals besides the human species. The first determination of the intrinsic rate of increase of an animal other than man was made by Leslie & Ranson (1940). They calculated the 'true rate of natural increase' of the vole, *Microtus agrestis*, from age-specific rates of fecundity and mortality determined under laboratory conditions. With the use of matrices Leslie has extended these methods and, as an example, calculated the true rate of natural increase of the brown rat, *Rattus norvegicus* (Leslie, 1945). The author is much indebted to Mr Leslie for having drawn his attention to the possible application of actuarial procedures to insect populations. He has been completely dependent upon him for the methods of calculation used in this paper.

Before proceeding to discuss the reasons for the particular terminology adopted in this paper, it is necessary first to consider the true nature of the parameter with which we are concerned.

* This investigation was carried out at the Bureau of Animal Population, Oxford University, during the tenure of an overseas senior research scholarship from the Australian Science & Industry Endowment Fund.

2. BIOLOGICAL SIGNIFICANCE OF THE INTRINSIC RATE OF NATURAL INCREASE

The intrinsic rate of increase is best defined as the constant 'r' in the differential equation for population increase in an unlimited environment,

$$dN/dt = rN,$$

or in the integrated form $N_t = N_0 e^{rt}$,

where N_0 = number of animals at time zero,
N_t = number of animals at time t,
r = infinitesimal rate of increase.

The exponent r is the difference between the birth-rate (b) and the death-rate (d) in the population ($r = b - d$). In some circumstances it may be more useful to know the finite rate of increase, i.e. the number of times the population multiplies in a unit of time. Thus, in a population which is increasing exponentially, if there are N_t individuals at time t then in one unit of time later the ratio

$$\frac{N_{t+1}}{N_t} = e^r$$
$$= \text{antilog}_e\, r = \lambda.$$

Hence the finite rate of increase (λ) is the natural antilogarithm of the intrinsic (infinitesimal) rate of increase.

Any statement about the rate of increase of a population is incomplete without reference to the age distribution of that population, unless every female in it happens to be producing offspring at the same rate at all ages, and at the same time is exposed to a chance of dying which is the same at all ages. In such an inconceivable population the age of the individuals obviously has no significance. In practice, a population has a certain age schedule both of fecundity and of mortality. Now a population with *constant* age schedules of fecundity and mortality, which is multiplying in an unlimited environment, will gradually assume a fixed age distribution known as the stable age distribution' (Lotka, 1925, p. 110). When this age distribution is established the population will increase at a rate $dN/dt = rN$. Thus the parameter r refers to a population with a stable age distribution. The consideration of rates of increase in terms of the stable age distribution was one of the most important advances in vital statistics. In any other sort of population the rate of increase varies with time until a stable age distribution is assumed. There is, for example, no simple answer to the question: what is the rate of increase of x newly emerged adult insects in an unlimited environment? The rate will vary with time as immature stages are produced until the population has a stable age distribution. The rate of increase in the first generation might be given, but that is a figure of limited value. On the other hand, the maximum rate that it can ever maintain over an indefinite period of time is given by the rate of increase in a population of stable age distribution. That rate is therefore the true intrinsic capacity of the organism to increase. Thompson (1931) rejected the use of the exponential formula in the study of insect populations in preference for a method of dealing with the rate of increase as a 'discontinuous phenomenon'. His paper should be consulted for the reasons why he considers a single index unsatisfactory in relation to the particular problems with which he was concerned.

If the 'biotic potential' of Chapman is to be given quantitative expression in a single index, the parameter r would seem to be the best measure to adopt, since it gives the intrinsic capacity of the animal to increase in an unlimited environment.* But neither 'biotic potential' nor 'true rate of natural increase' can be regarded as satisfactory descriptive titles. The word 'potential' has physical connotations which are not particularly appropriate when applied to organisms. There is a sense in which it might be better used with reference to the environment rather than the organism. Contrary to what it seems to imply, the 'true rate of natural increase' does not describe the actual rate of increase of a population at a particular point in time, unless the age distribution of that population happens to be stable. But it does define the intrinsic capacity of that population, with its given regime of fecundity and mortality, to increase. This point is clearly made by Dublin & Lotka (1925). More recently, Lotka (1945) has dropped the use of 'true rate of natural increase' for the more precise 'intrinsic rate of natural increase'. It would seem desirable that students of populations should adopt the same terminology, irrespective of the animals concerned, and as 'intrinsic rate of natural increase' is more truly descriptive of the parameter r than other alternatives, its use is adopted in this paper.

The intrinsic rate of increase of a population may be calculated from the age-specific fecundity† and survival rates observed under defined environmental conditions. For poikilothermic animals these rates vary with physical factors of the environment such as temperature and humidity. Furthermore, within any

* For a discussion of the relative merits of this and other parameters in human demography reference should be made to Lotka (1945).

† Fecundity rate is used to denote the rate at which eggs are laid by a female. Some eggs laid are infertile and so do not hatch. The percentage 'infertility' is included in the mortality rate of the egg stage. It is usual amongst entomologists to denote the percentage of fertile eggs as the 'fertility rate'. Demographers, on the other hand, use 'fertility rate' to denote the rate of live births. Since 'fertility rate' has this other usage in entomology the term 'fecundity rate' is used throughout this paper as synonymous with the 'fertility rate' of the demographers.

given combination of physical factors, the fecundity and survival rates will vary with the density of the animals. Hence it is possible to calculate an array of values of r at different densities. But particular significance attaches to the value of r when the fecundity and survival rates are maximal, i.e. when density is optimal, for this gives the maximum possible rate of increase *within* the defined physical conditions. *Between* the whole array of physical conditions in which the animal can survive there is a zone where fecundity and survival rates are greatest and where, therefore, the intrinsic rate of increase will be greatest too. The zone within which the intrinsic rate of increase is a maximum may be referred to as the optimum zone. This is an arbitrary use of the word optimum and it does not imply that it is always to the advantage of the animal to increase at the maximum possible rate. The maximum intrinsic rate of increase under given physical conditions has importance from two points of view. It has a theoretical value, since it is the parameter which necessarily enters many equations in population mathematics (cf. Lotka, 1925; Volterra, 1931; Gause, 1934; Crombie, 1945). It also has practical significance. The range of temperature and moisture within which the insect can multiply is defined most precisely by that range within which the parameter exceeds zero. This will define the maximum possible range. In nature the range of physical conditions within which the species may be found to multiply may be less, since it is possible that effects of density and interspecific competition may reduce this range, and also the range of the optimum zone. These considerations are, however, beyond the scope of this paper; some discussion of them will be found in a review paper by Crombie (1947).

There are some important differences in the orientation with which the demographer and the student of insect populations face their problems. In human populations the parameter r varies in different civilizations and at different times in one civilization, depending upon customs, sanitation and other factors which alter mortality and fecundity rates. The maximum possible value of r does not enter into most demographic studies. In a population which is growing logistically the initial rate of increase is theoretically the maximum intrinsic rate of increase, and this latter value can be determined indirectly by calculating the appropriate logistic curve. Lotka (1927) has done this for a human population and so arrived at an estimate of a physiological maximum for man. This has theoretical interest only. In insect populations, on the other hand, the maximum value for the intrinsic rate of increase does assume considerable theoretical and practical significance, as has already been pointed out. The entomologist can readily determine the maximum values and this is his obvious starting-point. But the determination of r at different stages in the population history of an insect, whether in an experimental population or in the field, offers many practical difficulties which have not yet been surmounted for any single species. The values which the entomologist has difficulty in determining are those which are most readily obtained for human populations. The crude birth-rates and crude death-rates of the population at specific stages in its history are precisely those indices with which the demographer works. His census data provides him with the actual age distribution which is something not known empirically for a single insect species. He can have a knowledge of age distribution even at inter-censal periods, and under civilized conditions he can also determine the age-specific rates of fecundity and mortality which were in operation during any particular year. In insect populations this is at present impossible; one can only keep a number of individuals under specified conditions and determine their age-specific rates of fecundity and survival, and from these data r can be calculated.

The fact that populations in nature may not realize the maximum value of their intrinsic rate of natural increase, does not negate the utility of this parameter either from a theoretical or a practical point of view. Having determined this parameter, the next logical step is to find out the extent to which this rate of increase is realized in nature. It is conceivable that some species, such as those which infest stored wheat or flour, may increase exponentially when liberated in vast quantities of these foodstuffs. This would imply that the insects could move out of the area in which they were multiplying with sufficient speed to escape density effects and that they had no gregarious tendencies. An exponential rate of increase may also occur in temperate climates in some plant-feeding species which only multiply in a short period of the year in the spring. In seasons with abundant plant growth the insect population may be far from approaching any limitation in the resources of the environment before the onset of summer retards the rate of increase. The population counts of *Thrips imaginis* in some favourable seasons in South Australia suggest such a picture (Davidson & Andrewartha, 1948).

3. CALCULATION OF THE INTRINSIC RATE OF NATURAL INCREASE

(*a*) *Experimental data required*

The calculation of r is based on the female population; the primary data required being as follows:

(1) The female life table giving the probability at birth of being alive at age x. This is usually designated l_x ($l_0 = 1$).

(2) The age-specific fecundity table giving the

mean number of female offspring produced in a unit of time by a female aged x. This is designated m_x.

In the calculation of the stable age distribution the age-specific survival rates (l_x) of both the immature stages and the reproductive stages are required. For the calculation of r the life table of the adult and only the total survival of the immature stages (irrespective of age) are needed. In practice, the age-specific fecundity rates m_x will be established for some convenient interval of age, such as a week. If N eggs are laid per female alive between the ages x to $x+1$ in the unit of time chosen, then m_x simply equals $\frac{1}{2}N$ when sex ratio is unity. It is assumed that this value occurs at the mid-point of the age group.

A numerical example is worked out for the rice weevil *Calandra* (*Sitophilus*) *oryzae* (L.) living under optimum conditions (29° C. in wheat of 14% moisture content). Data for the rates of development and survival of the immature stages, and the age-specific fecundity rates were obtained from Birch (1945*a*, *b*). The life table of adult females has not been determined experimentally, only the mean length of adult life being known. However, an estimate was obtained for purposes of these calculations by adapting the known life table of *Tribolium confusum* Duval (Pearl, Park & Miner, 1941) to *Calandra oryzae*, making the necessary reduction in the time scale. Since the mean length of life of *Tribolium confusum* in this life table was 198 days and the mean length of life of *Calandra oryzae* at 29° was 84 days, one '*Calandra* day' has been taken as equivalent to 2·35 '*Tribolium* days'. To this extent the example worked out is artificial, but, for reasons which will become evident later in the paper, it is unlikely that the error so introduced in the estimate of r is of much significance.

Before proceeding to outline direct methods of estimating r two other parameters must first be mentioned: the net reproduction rate and the mean length of a generation.

(*b*) *The net reproduction rate*

This is the rate of multiplication in one generation (Lotka, 1945) and is best expressed as the ratio of total female births in two successive generations. This we shall call R_0 and so follow the symbolism of the demographers. R_0 is determined from age-specific fecundity and survival rates and is defined as

$$R_0 = \int_0^\infty l_x m_x \, dx,$$

where l_x and m_x are as already defined.

The method of calculating R_0 is set out in Table 1. The values of l_x are taken at the mid-point of each age group and age is given from the time the egg is laid. Since the survival rate of the immature stages was 0·90 the life table of adults reckoned from 'birth', i.e. oviposition, was the product: l_x for adults $\times$ 0·90. Development from the egg to emergence of the adult from the grain lasts 28 days and 4·5 weeks is the mid-point of the first week of egg laying. The product $l_x m_x$ is obtained for each age group and the sum of these products $\Sigma l_x m_x$ is the value R_0. In this particular example $R_0 = 113{\cdot}6$. Thus a population of *Calandra oryzae* at 29° will multiply 113·6 times *in each generation.*

Table 1. *Showing the life table (for oviposition span) age-specific fecundity rates and the method of calculating the net reproduction rate* (R_0) *for* Calandra oryzae *at* 29° *in wheat of* 14% *moisture content. Sex ratio is equal*

Pivotal age in weeks (x)	(l_x)	(m_x)	($l_x m_x$)
4·5	0·87	20·0	17·400
5·5	0·83	23·0	19·090
6·5	0·81	15·0	12·150
7·5	0·80	12·5	10·000
8·5	0·79	12·5	9·875
9·5	0·77	14·0	10·780
10·5	0·74	12·5	9·250
11·5	0·66	14·5	9·570
12·5	0·59	11·0	6·490
13·5	0·52	9·5	4·940
14·5	0·45	2·5	1·125
15·5	0·36	2·5	0·900
16·5	0·29	2·5	0·800
17·5	0·25	4·0	1·000
18·5	0·19	1·0	0·190
			$R_0 = 113{\cdot}560$

The comparison of two or more populations by means of their net reproduction rates may be quite misleading unless the mean lengths of the generations are the same. Two or more populations may have the same net reproduction rate but their intrinsic rates of increase may be quite different because of different lengths of their generations. Consider, for example, the effect of moving the $l_x m_x$ column in Table 1 up or down by a unit of age, R_0 remains the same but it is obvious that the generation times are now very different. For these reasons the parameter R_0 has limited value and it must always be considered in relation to the length of the generation (T).

(*c*) *The mean length of a generation*

The relation between numbers and time in a population growing exponentially is given by

$$N_T = N_0 e^{rT}.$$

When T = the mean length of a generation, then from the definition of net reproduction rate $N_T/N_0 = R_0$, hence

$$R_0 = e^{rT},$$

and

$$T = \frac{\log_e R_0}{r}.$$

It follows that an accurate estimate of the mean length of a generation cannot be obtained until the value of r is known. For many purposes, however, an approximate estimate of T which can be calculated independently of r may be of use. Thus, although oviposition by the female is extended over a period of time, it may be considered as concentrated for each generation at one point of time, successive generations being spaced T units apart (Dublin & Lotka, 1925). For approximate purposes therefore it may be defined as

$$T=\frac{\Sigma x l_x m_x}{\Sigma l_x m_x}.$$

We may thus consider the figures for the product $l_x m_x$ given in the last column of Table 1 as a frequency distribution of which the individual items are each concentrated at the mid-point of each age group. The mean of this distribution is the approximate value of T. In this particular example

$$T=\frac{943{\cdot}09}{113{\cdot}56}=8{\cdot}3 \text{ weeks.}$$

If this were an accurate estimate of T we could proceed to calculate the value of r since, from the above equation relating R_0, r and T, we have

$$r=\frac{\log_e R_0}{T}$$

$$=\frac{\log_e 113{\cdot}56}{8{\cdot}30}=0{\cdot}57 \text{ per head per week.}$$

It will become evident in what follows that this is an underestimate of r owing to the approximate estimate of T. The procedure does, however, serve to illustrate the nature of the parameter, and in some cases where r is small it may be a sufficiently accurate means of calculation (cf. for example, Dublin & Lotka, 1925). We shall proceed in the next section to an accurate method for the calculation of r.

(*d*) *The calculation of* 'r'

A population with constant age schedules of fecundity and mortality will gradually approach a fixed form of age distribution known as the stable age distribution (p. 16). Once this is established the population increases at a rate $dN/dt=rN$ and the value of r may be calculated from the equation

$$\int_0^\infty e^{-rx} l_x m_x dx=1.$$

For the derivation of this formula reference must be made to Lotka (1925) and the bibliography therein. The usual methods of calculation may be found in Dublin & Lotka (1925, Appendix) or Lotka (1939, p. 68 *et seq.*). For high values of r, these methods may not be particularly satisfactory (Leslie & Ranson, 1940; Leslie, 1945, Appendix), and the computations, moreover, become very tedious. Some approximations to the rigorous procedures are justified in so far as the determination of the primary data which enter the above formula is of course subject to considerable error, arising from the normal variation in the organisms and conditions to which they are subjected in the experiments. It was considered that an estimate of r, calculated to the second decimal place, was sufficient in these circumstances. The following approximate method was therefore adopted. It has the merit of being both simple and fast.

As an approximation we may write

$$\Sigma e^{-rx} l_x m_x=1.$$

Here x is taken to be the mid-point of each age group and the summation is carried out over all age groups for which $m_x>0$. A number of trial values are now substituted in this equation, in each case calculating a series of values e^{-rx} and multiplying them by the appropriate $l_x m_x$ values for each age group. By graphing these trial values of r against the corresponding summation values of the left-hand side of the above expression, we may find the value of r which will make

$$\Sigma e^{-rx} l_x m_x \to 1.$$

The whole procedure is greatly simplified by the use of 4-figure tables for powers of e (e.g. Milne-Thomson & Comrie 1944, Table 9). Since these tables only give the values of $e^{\pm x}$ at intervals of 0·01 in the argument x up to $e^{\pm 6}$, it may be convenient to multiply both sides of the equation by a factor e^k in order to work with powers of e which lie in the more detailed parts of the table. Thus, in the present example, k was taken as 7:

$$e^7 \Sigma e^{-rx} l_x m_x = e^7$$

$$\Sigma e^{7-rx} l_x m_x = 1097.$$

A value of r was now sought which would make the left-hand side of this expression equal to 1097. The actual process of carrying out this simple computation is exemplified in Table 2. The summation of the expression is not carried beyond the age group centred at 13·5 because of the negligible contribution of the older age groups. It has already been mentioned that r is an infinitesimal rate of increase not to be confused with a finite rate of increase λ which equals antilog$_e$ r. In this particular example $r=0{\cdot}76$ and λ therefore has a value 2·14. In other words the population will multiply 2·14 times *per week*.

By reference to Table 2 it is clear that the relative weights with which the different age groups contribute to the value of r are given by the values $l_x m_x e^{7-rx}$ at each age group. It is of particular interest to observe the relation between values at successive age intervals (Table 3). The value of r is 56% accounted for by the first week of adult life. The first 2 weeks combined contribute 85% towards the final value and the first 3 weeks combined total 94%. The 13·5th week, on the other hand, contributes 0·02%. It

should not be inferred that adults 13·5 weeks old are of no importance since their eggs will eventually give rise to adults in the productive age categories. The biological significance of Table 3 is that the intrinsic rate of increase is determined to a much greater extent by the rate of oviposition in the first couple of weeks of adult life than by the total number of eggs laid in the life span of the adult, even although only 27 % of the total number of eggs are laid in the first 2 weeks. With

Table 2. *Showing the method of calculating r for* Calandra oryzae *at 29° by trial and error substitutions in the expression* $\Sigma e^{7-rx} l_x m_x = 1097$

Pivotal age group		$r=0{\cdot}76$		$r=0{\cdot}77$	
(x)	$l_x m_x$	$7-rx$	e^{7-rx}	$7-rx$	e^{7-rx}
4·5	17·400	3·58	35·87	3·53	34·12
5·5	19·090	2·82	16·78	2·76	15·80
6·5	12·150	2·06	7·846	1·99	7·316
7·5	10·000	1·30	3·669	1·22	3·387
8·5	9·875	0·54	1·716	0·45	1·5683
9·5	10·780	−0·22	0·8025	−0·32	0·7261
10·5	9·250	−0·98	0·3753	−1·09	0·3362
11·5	9·570	−1·74	0·1755	−1·86	0·1557
12·5	6·490	−2·50	0·0821	−2·62	0·0728
13·5	4·940	−3·26	0·0384	−3·39	0·0337
$\sum_{4\cdot5}^{13\cdot5} e^{7-rx} l_x m_x =$			1108		1047

r lies between 0·76 and 0·77 and by graphical interpretation = 0·762.

Table 3. *The contribution of each age group to the value of r when* $r=0{\cdot}76$

Pivotal age group (x)	$l_x m_x e^{7-rx}$	Percentage contribution of each age group
4·5	624·1	56·33
5·5	320·3	28·91
6·5	95·3	8·60
7·5	36·7	3·31
8·5	17·0	1·53
9·5	8·7	0·78
10·5	3·5	0·32
11·5	1·7	0·15
12·5	0·5	0·05
13·5	0·2	0·02
	1108·0	100·00

each successive week, eggs laid make a lessened contribution to the value of r. In this particular case this can be expressed by stating that for each egg laid in the first week of adult life it would require 2·1 times as many in the second week to make the same contribution to the value of r, $(2{\cdot}1)^2$ in the third week and $(2{\cdot}1)^{n-1}$ in the nth week. The ratio 2·1 : 1 is the ratio between successive weighting values e^{7-rx} (per egg) in Table 2. The importance of the first few weeks is further intensified by the fact that egg laying is at a maximum then. From these considerations it follows that in determining oviposition rates experimentally, the rates in early adult life should be found with the greatest accuracy. Of corresponding importance is the accurate determination of the pivotal age for the first age category in which eggs are laid. In the example being cited an error of half a week causes an error of 8 % in the estimate of r.

The calculations were repeated ignoring the adult life table. The value of r was then 0·77. Since the imposition of an adult life table only makes a difference of 1 % in the value of r it is evident that the life table is of little importance in this example. This is due to the fact already noted that the major contribution to the value of r is made by adults in early life, and during early adult life survival rate is at a maximum. The life table may assume quite a different importance in a species with a different type of age schedule of fecundity or when the value of r is lower.

4. THE STABLE AGE DISTRIBUTION

With a knowledge of the intrinsic rate of increase and the life table it is possible to calculate the stable age distribution and the stable female birth-rate of the population. Thus if c_x is the proportion of the stable population aged between x and $x+dx$, and b is the instantaneous birth-rate

$$c_x = be^{-rx} l_x,$$

and

$$1/b = \int_0^\infty e^{-rx} l_x dx.$$

For the usual methods of computation reference should be made again to Dublin & Lotka (1925). Mr Leslie has, however, pointed out to me another method of calculation which saves much of the numerical integration involved in the more usual methods. At the same time it is sufficiently accurate for our present purpose. If at time t we consider a stable population consisting of N_t individuals, and if during the interval of time t to $t+1$ there are B_t female births, we may define a birth-rate

$$\beta = B_t / N_t.$$

Then if we define for the given life table (l_x) the series of values L_x by the relationship $L_x = \int_x^{x+1} l_x dx$ (the stationary or 'life table' age distribution of the actuary),* the proportion (p_x) of individuals aged between x and $x+1$ in the stable population is given by

$$p_x = \beta L_x e^{-r(x+1)},$$

$$1/\beta = \sum_{x=0}^{m} L_x e^{-r(x+1)},$$

where $x=m$ to $m+1$ is the last age group considered in the complete life table age distribution. It will be noticed that the life table (l_x values) for the complete

* For a discussion of L_x see Dublin & Lotka (1936).

age span of the species are required for the computation of p_x and β. But where r is high it will be found that for the older age groups the terms $L_x e^{-r(x+1)}$ are so small and contribute so little to the value of β that they can be neglected.

The calculations involved are quite simple and are illustrated in the following example for *Calandra oryzae* at 29° (Table 4). Actually, in the present example, instead of calculating the values of L_x, the values of l_x were taken at the mid-points of each age group. This was considered sufficiently accurate in the present instance. It should also be pointed out that whereas only the total mortality of immature stages was required in the calculation of r, the age specific mortality of the immature stages is needed

Table 4. *Calculation of the stable age distribution of* Calandra oryzae *at* 29° *when* $r = 0{\cdot}76$

Age group (x)	L_x	$e^{-r(x+1)}$	$L_x e^{-r(x+1)}$	Percentage distribution $100\beta L_x e^{-r(x+1)}$	
0—	0·95	0·4677	0·4443150	54·740	95·5 % total immature stages
1—	0·90	0·2187	0·1968300	24·249	
2—	0·90	0·10228	0·0920520	11·341	
3—	0·90	0·04783	0·0430470	5·304	
4—	0·87	0·02237	0·0194619	2·398	4·5 % total adults
5—	0·83	0·01046	0·0086818	1·070	
6—	0·81	0·00489	0·0039609	0·488	
7—	0·80	0·002243	0·0017944	0·221	
8—	0·79	0·001070	0·0008453	0·104	
9—	0·77	0·000500	0·0003850	0·047	
10—	0·74	0·000239	0·0001769	0·022	
11—	0·66	0·000110	0·0000726	0·009	
12—	0·59	0·000051	0·0000301	0·004	
13—	0·52	0·000024	0·0000125	0·002	
14—	0·45	0·000011	0·0000050	0·001	
			$1/\beta = 0{\cdot}8116704$	100·000	

for the calculation of the stable age distribution. In this example the total mortality of the immature stages was 10 %—and 98 % of this mortality occurred in the first week of larval life (Birch, 1945*d*). Hence the approximate value of L_x for the mid-point of the first week will be 0·95 and thereafter 0·90 for successive weeks of the larval and pupal period (column 2, Table 4). The stable age distribution is shown in the fifth column of Table 4. This column simply expresses the fourth column of figures as percentages. It is of particular interest to note the high proportion of immature stages (95·5 %) in this theoretical population. This is associated with the high value of the intrinsic rate of natural increase. It emphasizes a point of practical importance in estimating the abundance of insects such as *C. oryzae* and other pests of stored products. The number of adults found in a sample of wheat may be quite a misleading representation of the true size of the whole insect population. Methods of sampling are required which will take account of the immature stages hidden inside the grains, such, for example, as the 'carbon dioxide index' developed by Howe & Oxley (1944). The nature of this stable age distribution has a bearing on another practical problem. It provides further evidence to that developed from a practical approach (Birch, 1946) as to how it is possible for *C. oryzae* to cause heating in vast bulks of wheat, when only a small density of adult insects is observed. It is not an unreasonable supposition that the initial rate of increase of insects in bulks of wheat may approach the maximum intrinsic rate of increase and therefore that the age distribution may approach the stable form. Nothing, however, is known about the actual age distribution in nature at this stage of an infestation.

5. THE INSTANTANEOUS BIRTH-RATE AND DEATH-RATE

We have already defined a birth-rate β by the expression

$$1/\beta = \sum_{x=0}^{m} L_x e^{-r(x+1)}.$$

This is not, however, the same as the instantaneous birth-rate (b) where $r = b - d$. In personal communications Mr Leslie has provided me with the following relationship between these two birth-rates.

$$b = \frac{r\beta}{e^r - 1}.$$

Thus, in the example for *C. oryzae*, we have $1/\beta = 0{\cdot}81167$ (Table 4), $r = 0{\cdot}76$ and thus $b = 0{\cdot}82$ and the difference between r and b is the instantaneous death-rate (d) $= 0{\cdot}06$.

The instantaneous birth-rate and death-rate are widely used by students of human populations. The insect ecologist is more likely to find greater use for the finite rate of increase λ (natural antilog$_e$).

6. THE EFFECT OF TEMPERATURE ON 'r'

As an illustration of the way in which the value of r varies with temperature and the corresponding changes in rate of development, survival and fecundity, an estimate of r for *C. oryzae* has been made for two temperatures (23° and 33·5° C.) on either side of the optimum (29°). The span of adult life at 23° is about the same as at the optimum 29° and so the same life table has been applied. Even although the egg laying is more evenly distributed throughout adult life the life table makes little difference to the value of r. Furthermore, the first 2 weeks of adult life carry a weight of 59 % of the total weight of all age groups in the determination of the value of r. For every egg laid in the first week of adult life it would require 1·5

times as many eggs in the second week to make the same contribution to the value of r, and 2·3 times as many eggs in the third week to have the same effect. The relative weight of each week decreases less with successive weeks at 23° than at 29°. This is associated with the lower oviposition rates and the longer duration of the immature stages at 23°.

At 33·5° egg laying ceases after the fourth week of adult life, the mortality of adults during these 4 weeks is not high and so the estimate of r obtained without a life table may not be very different from the true value.

Table 5. *Showing the values of l_x, m_x and the estimate of r for* Calandra oryzae *at* 23° *and* 33·5°

23°			33·5°		
Pivotal age in weeks (x)	l_x	m_x	Pivotal age in weeks (x)	l_x	m_x
0·5 . . . 6·5 Immature stages	0·90	—	0·5 . . . 8·5 Immature stages	0·25	—
7·5	0·87	9·0	9·5	0·25	6·0
8·5	0·83	11·0	10·5	0·25	3·5
9·5	0·81	11·5	11·5	0·25	3·0
10·5	0·80	12·0	12·5	0·25	1·0
11·5	0·79	11·5			
12·5	0·77	13·0	$r = 0·12$ per head per week		
13·5	0·74	11·5			
14·5	0·66	11·0			
15·5	0·60	10·0			
16·5	0·52	11·0			
17·5	0·45	12·5			
18·5	0·36	10·5			
19·5	0·29	11·5			
20·5	0·25	4·0			
21·5	0·19	2·0			

With adult life table $r = 0·43$ per head per week.
Without adult life table $r = 0·44$,, ,,

7. DISCUSSION

In order for a species to survive in a particular environment it may need to have evolved a certain minimum value for its intrinsic rate of natural increase. If its rate of increase is less than this it may succumb in the struggle for existence. It does not necessarily follow that the higher the intrinsic rate of increase the more successful will the species be. Evolution may operate to select species with an intrinsic rate of increase which is both large enough to enable them to compete successfully with other species and small enough to prevent a rate of multiplication which would exhaust the food supply in the environment. Whatever is the minimum necessary value of 'r' it could be attained along more than one route, since r has a number of component variables; the length of development of the immature stages, the survival rate of the immature stages, the adult life table and the age-specific fecundity schedule. These components enter into the value of r with various weights, and it is suggested in the discussion which follows that a knowledge of their relative contributions may provide a clue to the significance of the life patterns characteristic of different species. There is clearly a pattern in the seasonal environment too, which must be considered at the same time. A hot dry period, for example, may necessitate a prolonged egg stage. In an environment which has relatively uniform physical conditions all the year round, these complicating factors are at a minimum, e.g. a tropical forest or the micro-environment of a stack of wheat.

(1) Consider first the length of the immature stages (non-reproductive period) in relation to the span of egg laying and the age schedule of fecundity. The earlier an egg is laid in the life of the insect the greater is the contribution of that particular egg to the value of r. In illustration we may consider the age schedule of fecundity for *C. oryzae* at 29°. Since over 95 % of the value of r is determined by the eggs laid in the first 4 weeks of adult life (Table 3) we can, for purposes of illustration, ignore the remaining period.

At 29° the immature stages of *C. oryzae* last 4 weeks and the maximum rate of egg laying is 46 eggs per week (Table 1). Now the same value of r (0·76) is given in a number of imaginary life cycles by reducing the length of the immature stages along with a reduction in the rate of egg laying and alternatively by increasing both the length of the immature stages and the number of eggs laid (ordinary figures, Table 6). In Table 6 the age schedule of fecundity is kept proportionate in each case. In the extreme examples if the immature stages could develop in a week, an oviposition maximum of 5 eggs per week would give the same rate of increase as the imaginary insect which took 6 weeks to develop and had an oviposition maximum of 204 eggs per week. The imaginary life cycles have been calculated from the ratio (2·1 : 1) for successive weighting values (e^{7-rx}) in Table 2.

The question might now be asked, what determines the particular combination which the species happens to possess? In the specific example in question, if the larva took 6 weeks to develop the adult would need to lay 200 eggs per week. But it now becomes necessary to consider the behaviour pattern, for *C. oryzae* bores a hole in the grain of wheat for every egg which is laid. The whole process of boring and egg laying occupies about 1 hr. per egg. So that with this particular mode of behaviour 24 eggs per day would be an absolute maximum. There must of course also be some physiological limit to egg production. For a larger insect the physiological limit might be less restrictive provided that the size of the egg does not increase

proportionately with the size of the insect. In considering this possibility, ecological considerations are important, for *C. oryzae* is adapted to complete its development within a grain of wheat and a size limit is set by the length of the grain. There is, in fact, a strain which is found in maize kernels in Australia and this is considerably larger than the so-called 'small strain' (Birch, 1944). Furthermore, the larger insect would probably require a longer time to complete development (which is actually the relationship observed between the small and large strains) and this would operate to reduce the value of r. In considering the possibilities in the opposite direction, there is obviously a limit below which the length of development could not be reduced any further. A species of smaller size could doubtless develop in a shorter time and on this merit might be a more successful mutation. But the question then arises whether a smaller species could command muscles and mandibles of sufficient strength to chew whole grain. Grain-feeding species of beetles which are smaller than *C. oryzae* are in fact scavengers rather than feeders on sound grain. Thus it would seem that a balance is struck somewhere between the minimum time necessary for development and the maximum possible rate of egg laying, and this is conditioned by the behaviour pattern of the insect and the particular ecology of its environment.

For a maximum value of r the optimum age schedule of fecundity is one which has an early maximum. In an imaginary schedule for *C. oryzae* a concentration of 71 eggs in the first week of egg laying would give the same value of r (0·76) as 141 eggs distributed over 4 weeks.

Age schedule of fecundity of Calandra oryzae *at* 29°

Weeks	1	2	3	4	Total
Actual	40	46	30	25	141
Imaginary	71	0	0	0	71

The relative advantage of this type of fecundity schedule is less, the smaller the value of r. At 23° the value of r for *C. oryzae* is 0·43 and the eggs laid in the first week of adult life are worth $(1{\cdot}5)^{n-1}$ eggs in the nth week (compare this with the value of $(2{\cdot}1)^{n-1}$ when $r = 0{\cdot}76$). The actual oviposition time curve at 23° has no distinct peak as at 29° (Tables 1 and 5).

There is a wide variation in the nature of the age schedule of fecundity amongst different species of insects with perhaps the tsetse fly and the lucerne flea illustrating contrasting extremes. Whereas tsetse flies (*Glossina*) deposit single larvae spaced at intervals of time, the 'lucerne flea' (*Smynthurus viridis*) deposits its eggs in one or two batches of as many as 120 at a time (Maclagan, 1932). The particular advantage of this mode of oviposition must be tremendous, and is probably responsible in part for the great abundance of this collembolan and possibly other members of the same order, which, as a whole, are among the most abundant insects in nature. This is of course speculative and much more information is required before any generalizations can be made. Another interesting category are the social insects, since only one female of the population (in termites and the hive-bee) or a few (in social wasps) are reproductives. A theoretical consideration of the relative merits of one queen and many queens might throw more light on the evolution of these systems, especially as they relate to differences in behaviour.

The relation between the length of the pre-reproductive stages and the nature of the age-fecundity schedule is in part dependent upon the nature of the seasonal changes in the environment. Life histories may be timed so that the reproductive and feeding stages coincide with the least hostile season of the year. Diapause, aestivation and hibernation are some of the adaptations which ensure this. They have particular significance too in determining the age distribution of the initial population in the reproductive

Table 6. *Showing the actual relation between the length of the immature stages and the age schedule of fecundity for* Calandra oryzae *at* 29° (*black figures*) *and some theoretical possibilities which would give the same intrinsic rate of increase* ($r = 0{\cdot}76$). *The length of the immature stages is shown in the left of the table; figures in the body of the table are number of eggs per week*

	Pivotal age in weeks									
	0·5	1·5	2·5	3·5	4·5	5·5	6·5	7·5	8·5	9·5	Total
1 week		4	5	3	3	—	—	—	—	—	15
2 weeks			9	10	7	6	—	—	—	—	32
3 weeks				19	22	14	12	—	—	—	67
4 weeks					**40**	**46**	**30**	**25**	—	—	**141**
5 weeks						84	97	63	53	—	297
6 weeks							117	204	132	111	564

season. Consideration of this is left to a later section of the discussion.

(2) For the calculation of the maximum intrinsic rate of increase the life table of the species from deposition of the egg (or larva) to the end of egg-laying life in the adult must be known. The starting-point of this life table is thus the stage which corresponds to the point of 'birth'. Deevey (1947) has noted that the point of universal biological equivalence for animals is doubtless fertilization of the ovum. But, from the point of view of the number of animals in the population and for purposes of calculating r, a knowledge of pre-birth mortality is not required. For the calculation of r the life table beyond the end of reproductive life has no significance, but a knowledge of age-specific post-reproductive survival until the point of death is needed, on the other hand, for the calculation of the stable age distribution and the instantaneous birth-rate. This is evident from a consideration of the method of calculation shown in Table 4. The post-reproductive life assumes negligible significance in this particular example, but its importance in such calculations increases as r approaches a value of zero.

The relative importance of the survival pattern (i.e. the shape of the l_x curve) in determining the value of r is itself a function of r. When r is small its value may be dependent to a significant extent on the oviposition in late adult life, when it is large it is mostly determined by the oviposition rates of adults in early adult life. When the intrinsic rate of increase is high and the life table of the adult follows the typical diagonal pattern (e.g. Pearl *et al.* 1941) with no high mortality in early adult life, consideration of the adult life table is of little importance in calculating r. This is because survival rate is high in the ages which contribute most to the value of r. In species which have a low intrinsic rate of increase the life table may assume more significance in determining the value of that rate of increase. More data are required before the importance of this point can be established. The pattern of survival which gives a maximum value of r has its maxima in the pre-reproductive and early reproductive stages. A knowledge of total survival of the immature stages is of course essential in all cases. More attention might well be given by entomologists to securing life table data than has been given in the past. Without it no true picture of the intrinsic rate of increase can be obtained.

(3) There remains to be considered the age distribution of the population in relation to its capacity to increase in numbers. In a population in an unlimited environment the stable age distribution is the only one which gives an unvarying value of r. For this reason the stable age distribution is the only sound basis on which to make comparisons between different values for rates of increase (whether between different species or one species under different physical conditions). The actual age distribution of a population in nature may be quite different and its consideration is of importance in determining the initial advantage one form of distribution has over another. In an unlimited environment these initial differences in age composition are eventually ironed out. A population which initiates from a number of adults at the peak age of egg laying clearly has a higher initial rate of increase than one which starts from the same number in all different stages of development.

These considerations may be of most importance in temperate climates where there is a definite seasonal occurrence of active stages. The stage in which the insect overwinters or oversummers will determine the age distribution of the population which initiates the seasonal increase in the spring or in the autumn (whichever the case may be). The pea weevil, *Bruchus pisorum*, in California hibernates as an adult. With the first warm days in the spring the adults leave their overwintering quarters under bark and fly into the pea fields (Brindley, Chamberlin & Hinman, 1946). Following a meal of pollen they commence oviposition on the pea crops. This mode of initiating the spring population would be far more effective than one which started with the same number of insects in the egg stage. The overwintering adults begin their reproductive life at a much later age than the adults in the next generation. It would be of interest to know whether the age schedule of fecundity (taking the commencement of egg laying as zero age) is the same for both generations. This is a point which does not appear to have been investigated for insects which hibernate as adults. It is clearly of much importance in determining the intrinsic rate of increase of successive generations.

Overwintering as pupae must theoretically rank as the second most effective age distribution for initiating spring increase. Many species which overwinter as pupae would have a higher mortality if they overwintered as adults. The corn-ear worm, *Heliothis armigera*, for example, can hardly be conceived as overwintering as an adult moth in the North American corn belt. In the northern part of this belt even the pupae which are protected in the soil are unable to survive the winter. Recolonization evidently takes place each year from the warmer south (Haseman, 1931).

Overwintering in the egg stage (in hibernation or in diapause) is common in insects. Here again it is difficult to imagine the other stages of these orders as successfully hibernating. The grasshopper, *Austroicetes cruciata* (Andrewartha, 1944), and the majority of aphids are examples of this. A minority of aphid species are, however, able to overwinter as apterae by finding protection in leaf axils and similar niches (Theobald, 1926), some others are enabled to

survive as adults by virtue of their symbiosis with ants (Cutright, 1925). The relatively vulnerable aphids find protection in the nests of ants. The ants not only carry them to their nests, but feed them during the winter months and with the return of spring plant them out on trees again!

Overwintering as nymphs or larvae is a rarer phenomenon except with species which can feed and grow at low temperatures and so are not hibernators. The active stages of the lucerne flea, *Smynthurus viridis*, for example, can be found in the winter in Australia (Davidson, 1934). The seasonal cycle of the reproducing population commences with the first rains in autumn; this population being initiated with oversummering eggs. The eggs are the only stage which are resistant to the dryness and high temperatures of the summer months. Species of insects with hardy adult stages like the weevil, *Otiorrhynchus cribricollis* (Andrewartha, 1933), aestivate as adults. An interesting case of a butterfly, *Melitaea phaeton*, aestivating as a quarter-grown larva at the base of its food plant is described by Hovanitz (1941).

The preceding examples illustrate how the age distributions of initiating populations vary in seasonal species. This depends on the nature of the overwintering or oversummering stage. The particular stage may have been selected in nature not only by virtue of its resistance to unfavourable physical conditions but also in relation to its merits in initiating rapid establishment of a population in the spring and autumn. The calculation of the initial and subsequent rates of increase of populations with these different types of age distribution is considerably more complicated than the calculation of intrinsic rates of increase for populations with stable age distributions. This problem is not dealt with in this paper and the reader is referred to Leslie (1945, p. 207 *et seq.*) for an outline of the principles involved in such calculations.

The length of the developmental stages, the age schedule of fecundity, the life table of the species and the age distribution of initiating populations present a pattern which has adaptive significance for the species. The analytic study of the intrinsic rate of increase of a species (as exemplified by *Calandra oryzae*) may throw light on the evolutionary significance of the life pattern of different species. Such a study must necessarily be related to the behaviour pattern of the insect and the type of environment it lives in. Nor can the importance of effects of density and competition be overlooked. These are, of course, studies in themselves beyond the scope of this paper.

8. SUMMARY

The parameter known as the intrinsic rate of natural increase, which was developed for demographic analyses by A. J. Lotka, is introduced as a useful concept for the study of insect populations. It is suggested that for the sake of uniformity of terminology in population biology and for precision of definition, that the term 'intrinsic rate of natural increase' might be considered more appropriate than an alternative term 'biotic-potential' which is more frequently used in relation to insect populations. The intrinsic rate of natural increase is defined as the exponent 'r' in the exponential equation for population increase in an unlimited environment. The rate of increase of such a population is given by $dN/dt = rN$. The parameter r refers to the rate of increase of a population with a certain fixed age distribution known as the stable age distribution. Both the intrinsic rate of natural increase and the stable age distribution may be calculated from the age-specific survival rates (life table) and age-specific fecundity rates. The methods of calculation are exemplified with data for the rice weevil, *Calandra oryzae* (L.), and some adapted from the flour beetle, *Tribolium confusum* Duval. It is shown in this example that the intrinsic rate of natural increase is determined to a much greater extent by the rate of oviposition in the first 2 weeks of adult life than by the total number of eggs laid in the entire life time. The oviposition rates in the first 2 weeks account for 85 % of the value of r whereas only 27 % of the total number of eggs are laid in that time. With each successive week in the life of the adult, eggs laid make a lessened contribution to the value of r. The methods of calculation of r provide a means of determining the extent to which the various components—the life table, the fecundity table and the length of the pre-reproductive stages—enter into the value of r. It is suggested that analyses of this sort may provide a clue to the life patterns characteristic of different species.

The importance of the age distribution of populations which initiate seasonal increase in the autumn and spring is discussed. These age distributions depend on the nature of the overwintering or oversummering stage. It is suggested that this particular stage, whether it be adult, larva, pupa or egg, has been selected by virtue not only of its resistance to the unfavourable season, but also in relation to its merits in initiating rapid establishment of a population in the succeeding season.

It is shown how the value of r for *Calandra oryzae* varies with temperature. Four other parameters are also defined: the net reproduction rate, the mean length of a generation, the infinitesimal birth-rate and the infinitesimal death-rate. The methods of calculation of these parameters are also exemplified with data for *C. oryzae*.

9. ACKNOWLEDGEMENTS

Grateful acknowledgement is made to the Director of the Bureau of Animal Population, Oxford University, Mr C. S. Elton, for the facilities of the Bureau

which were placed at the author's disposal during his term there as a visiting worker. Mr Elton provided much encouragement during the investigation. It is a pleasure to acknowledge too the inspiration and help of Mr P. H. Leslie of the Bureau of Animal Population. His direction was indispensable in all mathematical and actuarial aspects of the paper and his critical examination of the manuscript was much to its advantage.

REFERENCES

Andrewartha, H. G. (1933). 'The bionomics of *Otiorrhynchus cribricollis* Gyll.' Bull. Ent. Res. 24: 373–84.

Andrewartha, H. G. (1944). 'The distribution of plagues of *Austroicetes cruciata* Sauss. (Acrididae) in relation to climate, vegetation and soil.' Trans. Roy. Soc. S. Aust. 68: 315–26.

Birch, L. C. (1944). 'Two strains of *Calandra oryzae* L. (Coleoptera).' Aust. J. Exp. Biol. Med. Sci. 22: 271–5.

Birch, L. C. (1945*a*). 'The influence of temperature on the development of the different stages of *Calandra oryzae* L. and *Rhizopertha dominica* Fab. (Coleoptera).' Aust. J. Exp. Biol. Med. Sci. 23: 29–35.

Birch, L. C. (1945*b*). 'The influence of temperature, humidity and density on the oviposition of the small strain of *Calandra oryzae* L. and *Rhizopertha dominica* Fab.' Aust. J. Exp. Biol. Med. Sci. 23: 197–203.

Birch, L. C. (1945*c*). 'The biotic potential of the small strain of *Calandra oryzae* and *Rhizopertha dominica*.' J. Anim. Ecol. 2: 125–7.

Birch, L. C. (1945*d*). 'The mortality of the immature stages of *Calandra oryzae* L. (small strain) and *Rhizopertha dominica* Fab. in wheat of different moisture contents.' Aust. J. Exp. Biol. Med. Sci. 23: 141–5.

Birch, L. C. (1946). 'The heating of wheat stored in bulk in Australia.' J. Aust. Inst. Agric. Sci. 12: 27–31.

Brindley, T. A., Chamberlin, J. C. & Hinman, F. G. (1946). 'The pea weevil and methods for its control.' U.S. Dept. Agric. Farmers' Bull. 1971: 1–24.

Chapman, R. N. (1931). 'Animal ecology with especial reference to insects.' New York.

Crombie, A. C. (1945). 'On competition between different species of graminivorous insects.' Proc. Roy. Soc. B, 132: 362–95.

Crombie, A. C. (1947). 'Interspecific competition.' J. Anim. Ecol. 16: 44–73.

Cutright, C. R. (1925). 'Subterranean aphids of Ohio.' Ohio Agric. Exp. Sta. Bull. 387: 175–238.

Davidson, J. (1934). 'The "lucerne flea" *Smynthurus viridis* L. (Collembola) in Australia.' Bull. Coun. Sci. Industr. Res. Aust. 79: 1–66.

Davidson, J. & Andrewartha, H. G. (1948). 'Annual trends in a natural population of *Thrips imaginis* Bagnall (Thysanoptera).' (In the Press.)

Deevey, E. S. (1947). 'Life tables for natural populations of animals.' Biometrics, 3: 59–60.

Dublin, L. I. & Lotka, A. J. (1925). 'On the true rate of natural increase as exemplified by the population of the United States, 1920.' J. Amer. Statist. Ass. 20: 305–39.

Dublin, L. I. & Lotka, A. J. (1936). 'Length of life.' New York.

Gause, G. F. (1934). 'The struggle for existence.' Baltimore.

Haseman, L. (1931). 'Outbreak of corn earworm in Missouri.' J. Econ. Ent. 24: 649–50.

Hovanitz, W. (1941). 'The selective value of aestivation and hibernation in a Californian butterfly.' Bull. Brooklyn Ent. Soc. 36: 133–6.

Howe, R. W. & Oxley, T. A. (1944). 'The use of carbon dioxide production as a measure of infestation of grain by insects.' Bull. Ent. Res. 35: 11–22.

Leslie, P. H. (1945). 'On the use of matrices in certain population mathematics.' Biometrika, 33: 183–212.

Leslie, P. H. & Ranson, R. M. (1940). 'The mortality, fertility and rate of natural increase of the vole (*Microtus agrestis*) as observed in the laboratory.' J. Anim. Ecol. 9: 27–52.

Lotka, A. J. (1925). 'Elements of physical biology.' Baltimore.

Lotka, A. J. (1927). 'The size of American families in the eighteenth century and the significance of the empirical constants in the Pearl-Reed law of population growth.' J. Amer. Statist. Ass. 22: 154–70.

Lotka, A. J. (1939). 'Théorie analytique des associations biologiques. Deuxième Partie. Analyse démographique avec application particulière à l'espèce humaine.' Actualités Sci. Industr. 780: 1–149.

Lotka, A. J. (1945). 'Population analysis as a chapter in the mathematical theory of evolution.' In LeGros Clark, W. E. & Medawar, P. B., 'Essays on Growth and Form', 355–85. Oxford.

Maclagan, D. S. (1932). 'An ecological study of the "lucerne flea" (*Smynthurus viridis*, Linn.)–I.' Bull. Ent. Res. 23: 101–90.

Pearl, R., Park, T. & Miner, J. R. (1941). 'Experimental studies on the duration of life. XVI. Life tables for the flour beetle *Tribolium confusum* Duval.' Amer. Nat. 75: 5–19.

Stanley, J. (1946). 'The environmental index, a new parameter as applied to *Tribolium*.' Ecology, 27: 303–14.

Theobald, F. V. (1926). 'The plant lice or the Aphididae of Great Britain.' Vol. 1. Ashford.

Thompson, W. R. (1931). 'On the reproduction of organisms with overlapping generations.' Bull. Ent. Res. 22: 147–72.

Thomson, L. M. Milne- & Comrie, L. J. (1944). 'Standard four-figure mathematical tables.' London.

Volterra, V. (1931). 'Leçons sur la théorie mathématique de la lutte pour la vie.' Paris.

AN ECOLOGICAL STUDY OF THE ENCHYTRAEID WORM POPULATION OF SEWAGE BACTERIA BEDS: SYNTHESIS OF FIELD AND LABORATORY DATA

By T. B. REYNOLDSON, *Department of Zoology, University College of North Wales, Bangor*

(With 3 Figures in the Text)

1. INTRODUCTION

In this paper, the third of a series, an attempt is made to resolve certain abnormal conditions of the enchytraeid worm population of the Huddersfield sewage bacteria beds by synthesizing field and laboratory data. A field study (Reynoldson, 1947*a*) revealed that the population of these beds was largely composed of *Enchytraeus albidus* Henle, a species rarely recorded from this habitat; while the common bacteria bed enchytraeid, *Lumbricillus* (=*Pachydrilus*) *lineatus* Müll., was scarce. Moreover, the total population of the Huddersfield beds was much smaller than normally occurs, and the vertical distribution within the beds was also atypical with the concentration below the 12 in. level. Regular sampling of the population showed that there was a marked seasonal fluctuation in numbers—a condition which has not been noted in populations of other beds. The routine beds at Cooper Bridge were the main subject of the field work, but two experimental beds, one (the Primary) treating sewage at a high rate of application, the other (the Secondary) treating sewage from the Primary bed, were also observed since they provided conditions contrasting with those of the routine beds.

The experimental work described in the second paper (Reynoldson, 1947*b*) is mainly concerned with evaluating the toxic property towards the worms, of the sewages fed to and leaving the three types of bed. By this means evidence was obtained of the relative mortality caused by the various kinds of sewage.

It was found that although each of the three bed types contained a numerically different population, the seasonal cycle of numbers followed parallel courses in the Cooper Bridge and Secondary beds; the operating portion of the Primary bed contained no enchytraeids. Since experiments indicated that conditions in the first two beds differed, it appeared that the seasonal cycle was, within limits, independent of the habitat, particularly as no seasonal variation in the toxicity of the sewage was detected. Therefore, the problems are considered under two heads: those dealing with (*a*) the fauna composition, total population and vertical distribution, which will be shown to be related to the strength of the sewage applied to the bed; (*b*) the seasonal cycle, which will be shown to be related to changes in the flora and fauna of the beds.

Although this paper deals with an artificial environment, some of the results, particularly those dealing with the seasonal cycle, have wider ecological application to theory and practice. This type of habitat has the merit of simplicity on the one hand, the case for which is admirably stated by Gause (1934); while on the other, it does not suffer from so many of the shortcomings inherent in laboratory studies of populations. It represents an environment which is open to natural colonization and which is exposed within limits (Lloyd, 1935) to the natural vagaries of the weather. By study of these unintended large-scale field experiments represented by the bacteria bed it is possible to disentangle the interactions of plants and animals and the relationship between animals of the same and different species more precisely than in complex natural habitats.

In the first paper (Reynoldson, 1947*a*) a broad similarity was drawn between the bacteria bed habitat and the wrack zone of the seashore. Interesting support for this suggestion is afforded by the recent publication of Backlund (1945) on the wrack fauna of Sweden and Finland. All the important bacteria bed genera except the chironomids occur in the wrack, while the enchytraeids *Lumbricillus lineatus* and particularly *Enchytraeus albidus* are characteristic of the community.

2. THE VALIDITY OF THE EXPERIMENTAL DATA

Before using the results of laboratory experiments to explain field data it is necessary to inquire how closely a comparison of laboratory and field conditions can be pressed. In this particular work (Reynoldson, 1947*b*) the most obvious and important difference lay in the continuous replacement of the sewage immediately surrounding the worm in the bed. This contrast is emphasized since Dr Antice Evans (unpublished thesis) has shown that both species, but particularly *Lumbricillus lineatus*, produce mucus under unfavourable conditions, and that this mucus

can afford protection against toxic substances. There is also a considerable body of evidence, summarized by Allee (1931), of similar protective mechanisms in other aquatic animals. Therefore, the experimental data for adult and young worms may have set the toxicity too low compared with actuality. To this extent bed conditions may be even less favourable than the experiments suggest. Evans (unpublished thesis) has also shown that clumping, a characteristic reaction of *L. lineatus* under certain conditions, also affords protection to the more central members; but the scarcity of the species at Huddersfield renders this factor unimportant. In regard to the experiments with eggs, the displacement factor was probably less important; in the case of *L. lineatus* the field effect of the sewage on the eggs could not be more disastrous since 100% inhibition was recorded in experiments. In many habitats animals are often able to exist in a niche which has properties differing from those of the macro-habitat. In laboratory studies such a niche may be difficult to provide, and consequently results may be misleading. But here little weight can be attached to this kind of misinterpretation because niches are few in the bacteria bed. The most important source is provided by the crevices and pitting of the clinker in which worms, and particularly the cocoons, may be sheltered from the direct flow of sewage. But even here complete wetting occurs due to condensation, and a considerable degree of diffusion of sewage into the crevices must occur.

3. ABUNDANCE AND VERTICAL DISTRIBUTION

(*a*) *Determinants of worm abundance*

Experimental data suggested that the toxicity of the Huddersfield sewage was a major factor in determining the relative sizes of the population in the three types of bed examined. The mortality resulting from this toxicity was assessed by immersing batches of 10 worms in a film of the particular sewage being tested and observing the number surviving after 7 days. Cocoons were also tested but were kept on pads of cotton-wool moistened with sewage. In both cases the sewage was changed daily. This abiotic 'resistance' of the three habitats has been expressed numerically in Fig. 1 and Table 1 for the adult, immature and egg stages of both species of worm by taking an average of the percentage mortality caused by the sewage fed to a bed and that, termed the effluent, leaving it (Reynoldson, 1947*b*, tables 1–3, 5–7). The limitation of this method of averaging is the assumption that the removal of toxicity is proportional to bed depth, whereas the chemical and bacteriological evidence of oxidation (Barritt, 1931; Wishart & Wilkinson, 1941) suggests that removal is more rapid in the surface layers. Therefore, this measurement of mortality is only approximate but may be relied upon to give the order of it. In the case of the eggs of *Enchytraeus albidus* the mortality expressed contains an inherent 10–15% loss, due to sterility which occurs even under favourable conditions. Fig. 1 also records the population size in each of the three beds at the levels sampled as the number of worms taken in 1 week averaged over a period of 1 year.

It is clear that for both species the early developmental stages were most adversely affected by the toxicity, the adults less so. There is also a marked contrast between the ability of the two species to tolerate Huddersfield sewage; *E. albidus* has a decided advantage at every stage, but particularly during egg development. There is little doubt that this contrasted reaction explains the dominance of *E. albidus* in these beds and the paucity of *Lumbricillus lineatus*.

Comparison of the mortality in different beds attributed to toxicity suggests that the Primary bed should carry the smallest population of both species, the Secondary bed the largest and the Cooper Bridge beds a population intermediate in size. Considering *Enchytraeus albidus* first, although the Primary bed provides a habitat apparently only slightly less favourable than the Cooper Bridge beds, in degree represented by a 10% higher failure of egg development, there is a marked difference in the populations. The routine sampling showed that this species was absent from the Primary bed to a depth of 12 in. and six samples from 36 in. were also negative; yet a fairly large population inhabited the Cooper Bridge beds. The reason for the discrepancy must be sought elsewhere, and examination of actual bed conditions seemed to provide the answer. Reynoldson (1941, 1942) showed that the high flow of sewage to the Primary bed produced a considerable depression in the population of *Psychoda alternata* Say. Now the larvae of these flies are instrumental in promoting aerobic oxidation of the sewage by devouring accumulations of organic debris and fungi which otherwise block the interstices of the media. The scarcity of larvae in the Primary bed resulted in an accumulation of such material and the production of septic conditions. Thus the actual environmental conditions were probably sufficiently different to account for the contrast in the worm populations. Confirmation that the conditions in the Primary bed actively precluded the worm's presence was obtained by sampling in a small area immediately surrounding the central column of the distributor, which was not wetted by sewage. The results (Reynoldson, 1947*a*) showed that there was a small but persistent population of *Enchytraeus albidus* in this area which can have been prevented from extending into the rest of the bed only by a physico-chemical barrier set up by the application of sewage.

The presence of an overall larger population of *E. albidus* in the Cooper Bridge beds compared with the Secondary bed was contrary to expectation based on laboratory data. In seeking an explanation, the history of the two habitats cannot be ignored. The former have been in operation since 1910, whereas the latter commenced only in November 1938. Thus the population of the Secondary bed was of very recent origin, and the worms had had only one breeding season in which to build up numbers prior to the commencement of sampling; strict comparison is therefore invalidated. Close observation of the more recent population was made during 1941, 1942 and less extensive examination up to 1946 and, although an impression was received that numbers were growing, the point cannot be pressed. But the fact that this population had increased at the 6 in. level so rapidly as to equal the corresponding Cooper Bridge population is a firm indication of the probable ultimate result, one which would bring laboratory evidence and field criteria into line. The ability to penetrate more effectively into the uppermost zone of the Secondary bed, the one which experiments suggest was the more favourable, is clearly shown, since 24% of the upper population existed here compared with a corresponding figure of 2% for the Cooper Bridge beds. Thus, although the laboratory and field data are at some variance for this species, there are sound reasons for considering that both are valid and that the toxicity of the sewage was the main factor in determining the relative sizes of the three populations; absolute size was influenced by additional factors.

In the case of *Lumbricillus lineatus* there is more general agreement between field and laboratory results; perhaps a reflexion that here the ages of the populations were not so important because of the highly unfavourable conditions for permanent colonization. The inability of the eggs of this species to make progress in any Huddersfield sewage must be an overriding factor in denying a foothold. The presence of small numbers of worms in the Cooper Bridge beds from time to time, and their absence in the Primary bed despite the superficial similarity in conditions, is explained on the same grounds as the corresponding discrepancy with *Enchytraeus albidus*. It should be noted that *Lumbricillus lineatus* also occurred in the central niche referred to above. The relative abundance of the worms at the 6 in. level in the three beds agrees well with expectation, but the large numbers at the 12 in. level in the Secondary bed were unexpected and raise the question whether or not this species was able to breed in any of the beds. Laboratory experience suggests that breeding could not occur. It is in resolving such a point that the presence of an ecological niche becomes important. The improbability of worms depositing cocoons in places free from contact with sewage has been pointed out (§2). The fate of cocoons in the field was demonstrated by selecting three pebbles from the Leeds beds with attached cocoons containing eggs in an early developmental stage. Two pebbles were placed in the Cooper Bridge beds at a depth of 6 in., orientated so that the cocoons were uppermost in one case and on the lower face in the other; the third was retained as a control. They were removed after 8 days and it was found that of the 29 eggs contained in the cocoons on the upper face, 23 failed to develop and 6 were elongated but had died at this stage. The cocoons on the lower surface contained 30 eggs, of which 28 failed to develop but 2 had done so into active worms; the control showed 100% development. It is probably incorrect to conclude from this test that the eggs of *L. lineatus* are able to develop in any numbers in the bed, because the pebbles had only been in for a short time and conditions on their surfaces would not be so deleterious as on the permanent media. On the other hand, the Huddersfield clinker is much pitted and provided with concavities which may escape direct wetting with sewage, but diffusion is probably sufficient to prevent development. If this species is unable to breed in the Huddersfield beds its occurrence must be explained in some other way. An examination of the incidence of the worm showed that it occurred in the surface layers of the Cooper Bridge and Secondary beds over the same period. A careful review of possible underlying factors showed that the appearance of *L. lineatus* coincided with periods of heavy rainfall producing flood water at the sewage works. It is suggested that the worms were transported to the beds by the flood water, which washed cocoons and worms from the margins of streams and ponds some distance from the sewage works. The only difficulty in the way of the suggestion is the large number of worms which must be washed in, but this may disappear when more is known of the abundance of these worms in their natural habitat. Their occurrence at the 12 in. level in the Secondary bed was less related to rainfall and the validity of these samples, as reflecting the bed population, is raised, for the following reasons: (*a*) the numbers taken were large if the population was non-breeding; (*b*) the decline occurred at the time of the change in sampling technique (Reynoldson, 1947*a*); (*c*) it was not related to peak discharges of solids (§5). The data relating to (*a*) suggest that *L. lineatus* was unable to breed in the Secondary bed. If inability to breed is accepted it follows that the population at the 12 in. level was derived from flood water. In this circumstance it seemed very large, even if the worms persisted and the intermittent additions were cumulative. The most reasonable explanation of the high numbers seems to be the attraction which a small area of bed, protected from the down flow of sewage, exerted on

this species, an attraction not reflected by *Enchytraeus albidus*. As soon as this niche was removed by the adoption of the modified sampling method the worms were dispersed; close observation during 1941–2 suggested that the numbers of *Lumbricillus lineatus* remained small.

(*b*) *Determinants of the vertical distribution of* Enchytraeus albidus

The surface layers of a bacteria bed usually carry the heaviest population of insect larvae and enchytraeid worms (*Lumbricillus lineatus*) attracted by the concentration of algae, fungi, bacteria and organic debris, the food of these organisms (Fair, 1934; Lloyd, Graham & Reynoldson, 1940; Reynoldson, 1941; Tomlinson, 1941; Heukelekian, 1945). This zone also has easiest access to air and this factor may be an important determinant because sewage is usually devoid of oxygen. Thus the fact that only 2 % of the upper population of *Enchytraeus albidus* occurred in this topmost zone in the Cooper Bridge beds is clearly anomalous; the corresponding figure for the Secondary bed was 24 % (Fig. 1). The explanation may simply be that *E. albidus* prefers a lower zone. There is no direct evidence on this point for bacteria beds, but in natural habitats this is not the case, as it occurs most abundantly in the upper 2–3 cm. (Moszynski, 1930).

It seems clear that low temperature was not the cause. Experience with *Lumbricillus lineatus* showed that only during very cold weather, when the bed surface temperature fell below 6° C., did a downward migration occur. Such a factor was too intermittent to produce the condition at Huddersfield, particularly as *Enchytraeus albidus* seems to be more tolerant of cold than *Lumbricillus lineatus* (Reynoldson, 1943).

Although competition with larvae of the fly *Psychoda alternata* for food and space is most severe in the topmost zone this factor is only operative between April and November inclusive (Golightly, 1940; Reynoldson, 1941, 1942), and therefore cannot account for the low numbers during the winter. There is little doubt that the toxic properties of the Huddersfield sewage produced the anomalous distribution—not only is egg development inhibited but the sewage is also toxic to young worms (Table 1) and may also produce an avoiding reaction in adults. The higher proportion of worms in the top zone of the Secondary bed, as compared with the Cooper Bridge beds, may also be accounted for by a difference in toxicity, because the latter treats a sewage already partially oxidized, in the Primary bed. This tendency suggests

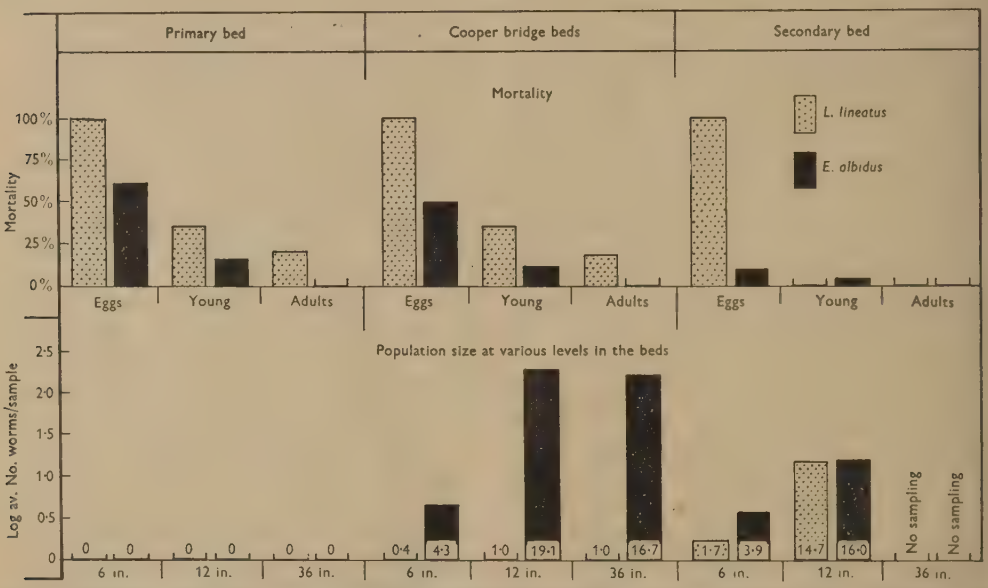


Fig. 1. Mortality in the Primary, Cooper Bridge and Secondary beds, and the enchytraeid worm populations at the various levels in the beds. Population size is shown as the logarithm of the average number per sample; the arithmetical average is also recorded at the foot of each block.

that with a more normal sewage *Enchytraeus albidus* would have a similar distribution to *Lumbricillus lineatus*. It has been pointed out (Reynoldson, 1947*b*) that the intermittent acidity of the Huddersfield sewage may play a subordinate part in the zoning of the Cooper Bridge population, but not in the Secondary bed.

The rapid stabilization of the worm population at a depth of 12 in. in the Cooper Bridge beds supports the view that the destruction of toxic substances was not uniform with depth but occurred more rapidly in the surface layers of media. This is in agreement with the work of Key & Etheridge (1934) who demonstrated that such substances as phenols, catechol, thiosulphate and thiocyanates could be completely oxidized by treatment in a bacteria bed. And, moreover, most were broken down in the upper layers, 69% of the total oxidation occurring in the top 13 in. of a bed 5 ft. 6 in. deep. A similar rate of oxidation in the Huddersfield beds would account for the distribution of *Enchytraeus albidus* which has been observed, and such an explanation is probably the correct one.

Table 1. *Summary of the percentage mortality of* Enchytraeus albidus *and* Lumbricillus lineatus *in the three sewage bed types due to toxicity of the sewage; figures in italics are not actual averages but take into account accidental death* (*Reynoldson*, 1947*b*)

	Primary bed		Cooper Bridge beds		Secondary bed	
	E. albidus	*L. lineatus*	*E. albidus*	*L. lineatus*	*E. albidus*	*L. lineatus*
Adults	1·0	20·5	0·0	18·0	0·0	0·0
Young	15·5	35·5	11·0	*35·5*	6·0	0·0
Eggs	61·0	100·0	50·0	100·0	22·0	100·0

4. DETERMINANTS OF THE SEASONAL CYCLE OF *ENCHYTRAEUS ALBIDUS*

A critical account of the trapping method and the seasonal cycle was given in detail in the first paper (Reynoldson, 1947*a*). In brief, the population showed a winter maximum followed by a rapid decline in the spring and a summer minimum.

The spring treatment of the Cooper Bridge beds with creosote to control the psychodid flies had only a slight effect on the worms, confined to those in the topmost few inches of clinker. It did not influence the seasonal cycle, particularly the spring decline which occurred before the treatment. Inspection of the rainfall and worm population peaks did not suggest any connexion similar to that discovered for *Lumbricillus lineatus*. Such a result probably means that the numbers of *Enchytraeus albidus* washed in were too small to produce a detectable increase in the population.

It is tempting to explain the eclipse of *E. albidus* as the result of unsuccessful competition with *Psychoda alternata*, particularly as the rise of the insect was coincidental with the decline of the worm. But there are several indications that competition for food and space do not provide the solution. The most significant is the distribution of the fly larvae, for in the Huddersfield beds they are concentrated towards the surface (Golightly, 1940; Reynoldson, 1941) above the main zone of *Enchytraeus albidus*. Furthermore, if such competition occurred it could hardly cause the sudden and total collapse (Reynoldson, 1947*a*), for there are many 'crumbs falling from the table' of the larvae. It is also some indication that *Lumbricillus lineatus*, whose food habits are identical with those of *Enchytraeus albidus*, is able to withstand the more vigorous competition of the chironomid larvae *Metriocnemus hygropetricus* Kieffer (= *longitarsus* Goetghebuer) and *Hydrobaenus* (= *Spaniotoma*) *minimus* (Mg.) (Lloyd *et al.* 1940). Finally, the recovery of the worms began in October and November, when the population of *Psychoda alternata* was as high as during the spring collapse.

The abruptness of the decline and its timing, the end of April in the Cooper Bridge beds and the end of May in the Secondary bed, suggest probable causes. The first feature shows clearly that it was an actual loss of worms which occurred, because although the intensity of breeding was falling at the time, even if breeding had ceased completely, the population would not decline so rapidly. Moreover, even if a steady drain on the population could be demonstrated, the rapidity of the collapse would compel further explanation.

The timing of the collapse is significant because, following the spring rise of the psychodid population, there is a profound change in the volume of fungus adhering to the clinkers. The sequence of events has been described in full (Reynoldson, 1942). Briefly, the feeding activities of the larvae strip the clinker of the slimy growth of bacteria, fungi and winter accumulation of sludge, and the resultant flocculent humus and various debris are gradually carried down the bed, ultimately passing out with the effluent. Such removal of winter accumulations is a general feature of bacteria beds and is technically referred to as the spring off-loading of solids. When this occurs

the worms literally have their feeding ground removed under them, and a large number still clinging to the solids are washed away in the effluent. Washing out of *Lumbricillus lineatus* also occurred in the Leeds beds (Reynoldson 1939*a*), but the population was so vast here that no decrease was detected.

The limited fauna at Huddersfield simplifies analysis of this factor, attention being confined to the Secondary bed for which most data are available. Timing is all-important and the two-stage collapse in the Secondary bed (Reynoldson, 1947*a*, fig. 4) enables a double check to be made. Table 2 records the relevant data of average worm numbers at 6 and 12 in.

Table 2. *Secondary bed—a record of the number of* Enchytraeus albidus *taken in the food bags averaged for* 6 *and* 12 *in. levels, the number of psychodid flies* (Psychoda alternata *and* P. cinerea) *emerging from* 1 *sq.ft. of bed surface and the solids in the effluent. The latter record is based on hourly samples taken over a* 24 *hr. period once weekly and is given in parts per* 100,000 *of effluent*

Week ending	No. of worms	No. of flies	Solids in effluent (parts per 100,000)
20 Mar.	75	5	—
28 Mar.	80	6	1·40
3 Apr.	69	176	0·85
10 Apr.	31	198	2·50
17 Apr.	16	152	0·95
24 Apr.	30	15	1·10
1 May	14	521	2·30
8 May	10	198	0·85
15 May	27	258	1·90
22 May	82	318	2·70
29 May	17	222	0·75

and the number of *Psychoda alternata* and *P. cinerea* Banks emerging from 1 sq.ft. of bed surface (Reynoldson, 1941), and the solids in the effluent, during the critical period (see also Fig. 2). Three peak discharges of solids are shown, on 10 April, 1 May and 22 May and the two largest of these were in close time relation to the two main drops in worm abundance. Even the solids peak on 1 May can be associated with a minor decline in the worm population. A more precise timetable cannot be expected because the figures for solids discharge are based on samples taken once weekly over a period of 24 hr., thus they may touch the beginning, the middle or the end of a peak discharge. Field observations suggested that the two main discharges related to different phases of the off-loading. The one occurring about 10 April was unaccompanied by any reduction in the film adhering to the top 8 in. of clinker, and must have originated from breakdown of film lower in the bed. The discharge on 22 May was accompanied by a complete disintegration and disappearance of the upper film. Lloyd (1943*b*) showed that peaks in the solids discharge and in the psychodid population at Huddersfield were correlated, and Table 2 records a similar agreement between flies and solids. Presumably the time lag between the scouring of the media by larvae and washing out of the humus equals approximately the interval occupied by pupation and emergence of the imagos. Referring now to the Cooper Bridge beds, although precise data of the same kind are not available, the use of creosote some 2 weeks after the collapse of the worm population is a sure indication that it occurred about the same time as the initial increase in the flies. Whether the peak discharges occur close together or at wider intervals depends largely on the closeness of the cycles of fly generations (Lloyd, 1943*b*), and there is no contradiction in the two-stage collapse of the worms in the Secondary bed and the single stage in the Cooper Bridge beds. Incontestable proof of this relationship requires daily estimates of the solids discharge and the accompanying worms, but convincing circumstantial evidence is given by the dense masses of worms which are found in the final settling tanks at the time of the spring off-loading.

Since off-loading is not confined to the spring, but occurs with a certain rhythm throughout the year associated with pulsations of the fly population (Lloyd, 1943*b*), it might be expected to influence the worm population and perhaps account for the apparently erratic fluctuations (Reynoldson, 1947*a*, fig. 4). Accordingly, Fig. 2 was constructed to show the number of *Enchytraeus albidus* taken at the 12 in. level and the solids discharged from the Secondary bed during the period of the worms' occurrence. The main depressions in worm abundance (including the spring period) have been numbered (1)–(8), while the peak discharges have been lettered (*a*)–(*i*). With two exceptions, (*b*) and (*c*), the peak discharges occurred either the previous or the same week as the drops in the worm population. The first exception can be discounted, because worms were already few at the time; while the second, (*c*), occurred one week after the decline of 20 December. In view of the sampling method for solids this is probably as close a relationship as could be expected and suggests that the fluctuations in worm numbers were caused by the solids discharge. The severity of the depressions cannot be related to the volume of discharge recorded; the data are inadequate to demonstrate such a relationship. This is indicated by the fact that the main discharges in the spring were not outstandingly high according to the records. Some measure of the drain on the worm population was given by straining the effluent from the Secondary bed (Reynoldson, 1947*a*, table 4). An average figure indicated that daily losses from the bed amounted to nearly 19,000 worms and

28,000 cocoons containing some 100,000 eggs. Losses much less than these would be a severe drain on such a small population. It should be noted that the earlier samples were taken before the spring off-loading, and do not represent maximum losses. It is most probable that there was a constant drain on the population, due partly to a mechanical washing out and partly to the tendency of the worms to cling to debris as it was swept down the bed. This would reach a maximum during peak discharges of solids. The failure of the worm to make a rapid, partial recovery, despite the presence of immature worms in the beds must be attributed to this constant drain on the population; while the prolonged delay may be attributed to the lower summer breeding rate (Reynoldson, 1947*a*). A slight recovery did occur in the Cooper Bridge beds but it was only of short duration.

Regarding the general problem of loss by washing out, the small population of *E. albidus*, found in the central area of the Primary bed and not subjected to a flow of sewage (Reynoldson, 1947*a*), persisted in the topmost zone during the summer—a period when the worms could not be found in the corresponding zone of the beds treating sewage.

5. THE BACTERIA BED COMMUNITY

An account of competition in the Leeds beds has been given by Lloyd *et al.* (1940) and Lloyd (1943*a*), and, although conditions are relatively simple here, the Huddersfield beds afford an even simpler community. Much more is known of the Secondary bed and its operation may be looked upon as a field experiment in ecology. The flora consists largely of a species of the fungus *Oospora* (Fungi Imperfecti), together with a small amount of bacteria in the form of a slimy zoogloea. The macro-fauna is dominated by the fly *Psychoda alternata* with the worm *Enchytraeus albidus* the second most numerous organism. There are few definitive predators and even spiders are scarce. The influence of parasitic Hymenoptera is also slight and unlikely to have any important effect on the sewage flies: Lloyd (1943*a*) recorded these parasites from the Leeds beds in the proportion of 1:12,000 emerging flies with an annual fluctuation of 1:11. Table 3, taken from Reynoldson (1941), records the larger organisms taken in 1 year from the Secondary bed at Huddersfield and illustrates the dominance of one species. Here then a simple

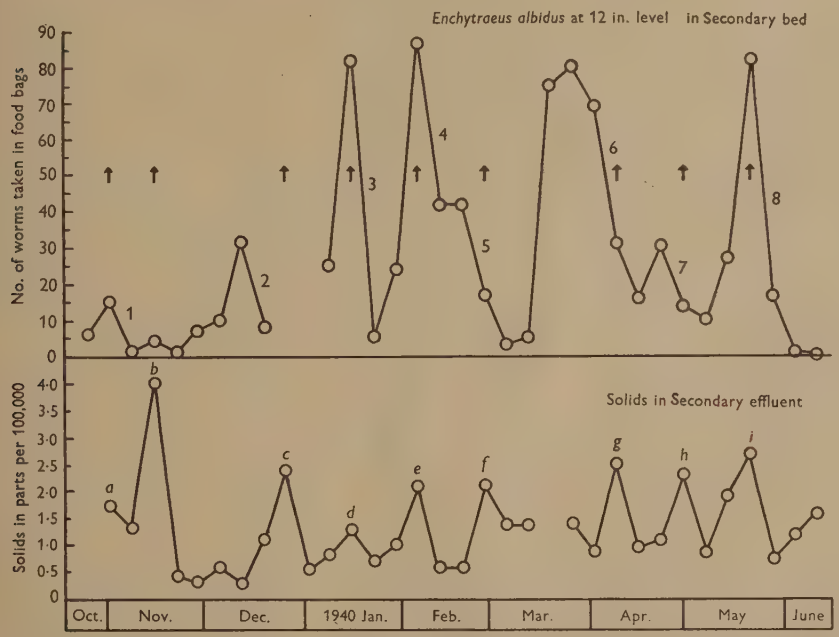


Fig. 2. Data from the Secondary bed to show the relationship between solids discharged and declines in the worm population. Solids peaks are lettered *a* to *i* and also indicated in the graph of *Enchytraeus albidus* by arrows; major declines in the worm population are numbered 1 to 8.

relationship between plant and animal (*Psychoda alternata*) exists, with little interference from predators and parasites. Under laboratory conditions the plant feeder might be expected to eat out its food supply and then perish. But in the bed quite a different result was obtained. The important data are summarized in Table 4 and Fig. 3 which record bed temperature, growth rate of *Oospora*, the size of the *Psychoda alternata* population and the relative numbers of *Enchytraeus albidus*.

Records of temperature, fungus and fly are taken from Reynoldson (1941, 1942). With the exception of temperatures, which are based on fortnightly averages of daily readings, the data are fortnightly averages of weekly estimates. Unfortunately, each type of record is not available over the same year, thus in 1939–40 estimates of the fungus were not made, and in 1941–2 worms were not sampled. But the general picture emerges clearly; records of the fly are given for both 1939–40 and 1941–2 so that details of the fly-fungus and fly-worm relationships can be examined. The fungus records related to rate of growth achieved per 56 sq. in. of bed surface and not the quantity in the bed at any given time. This growth was cumulative

Table 3. *Total numbers of macro-organisms taken in the Secondary bed over 1 year (Oct. 1939—Oct. 1940) by weekly trapping. (From Reynoldson, 1941)*

Oligochaeta Enchytraeidae		Diptera				Coleoptera			Araneida
		Psychodidae			Borboridae		Hydrophilidae		Linyphiidae
E. albidus	*L. lineatus*	*P. alternata*	*P. cinerea*	*P. severini*	*Limosina* spp.	Staphylinidae	*Helophorus* spp.	*Cercyon ustulatus*	
1107	908	10,152	103	12	16	12	14	80	25

Table 4. *Summary of the data for the Secondary bed community; fungus, fly and worm figures are fortnightly averages of weekly data. The fortnightly periods relate strictly to 1941–2—those for 1939–40 are within ± 2 days according to date*

Date	Temperature (° C.) 1941–2	Temperature (° C.) 1939–40	Growth rate of *Oospora* (wt. in g. per 56 sq.in.) (1941–2)	No. of *Psychoda alternata* per sq.ft. 1941–2	No. of *Psychoda alternata* per sq.ft. 1939–40	No. of *Enchytraeus albidus* in food bags, 1939–40 (6 + 12 in. level)
11–25 June	17·8	19·2*	—	450	350*	0*
26 June–9 July	19·3	18·4	0·35	225	243	0
10–23 July	19·6	18·5	0·53	373	260	0
24 July–6 Aug.	18·4	19·6	0·24	192	610	0
7–20 Aug.	16·0	16·7	0·34	194	210	0
21 Aug.–3 Sept.	17·0	18·2	0·61	213	88	0
4–17 Sept.	18·3	16·1	0·66	103	129	0
18 Sept.–1 Oct.	18·0	14·9	0·36	61	324	0
2–15 Oct.	16·4	14·4	0·34	327	405	1
16–29 Oct.	12·5	—	0·56	124	335	3
30 Oct.–12 Nov.	11·4	12·5	0·63	303	228	9
13–26 Nov.	11·7	12·5	0·78	62	180	4
27 Nov.–10 Dec.	11·6	9·9	0·40	56	42	9
11–24 Dec.	10·2	10·6	0·64	10	3	22
25 Dec.–7 Jan.	8·8	6·9	0·73	14	17	—
8–21 Jan.	9·2	8·5	0·76	8	2	56
22 Jan.–4 Feb.	9·3	7·7	0·38	0	0	25
5–18 Feb.	9·2	6·9	0·67	0	1	72
19 Feb.–4 Mar.	8·9	7·8	0·61	2	21	34
5–18 Mar.	8·2	9·7	0·89	3	6	5
19 Mar.–1 Apr.	11·0	10·4	1·38	5	81	90
2–15 Apr.	11·0	11·9	1·38	57	210	56
16–29 Apr.	13·0	12·2	1·95	115	262	48
30 Apr.–13 May	13·6	16·1	1·76	508	224	24
14–27 May	15·9	17·9	0·58	334	264	70
27 May–10 June	14·9	19·6	0·38	473	575	10

* 11 June to 15 Oct. refers to 1940. 2 Oct. to 31 Dec. refers to 1939. 1 Jan. to 10 June refers to 1940.

when the fly population was small. Owing to the differential reaction to temperature of the fungus and fly it was found that when the bed temperature was below 10° C., i.e. during the winter months, the fly temperature rose above 10° C., there was a burst of fungus growth lasting 4 weeks and considerable accumulation; the fly recovered more slowly. Complete collapse of the fungus followed as a result of the

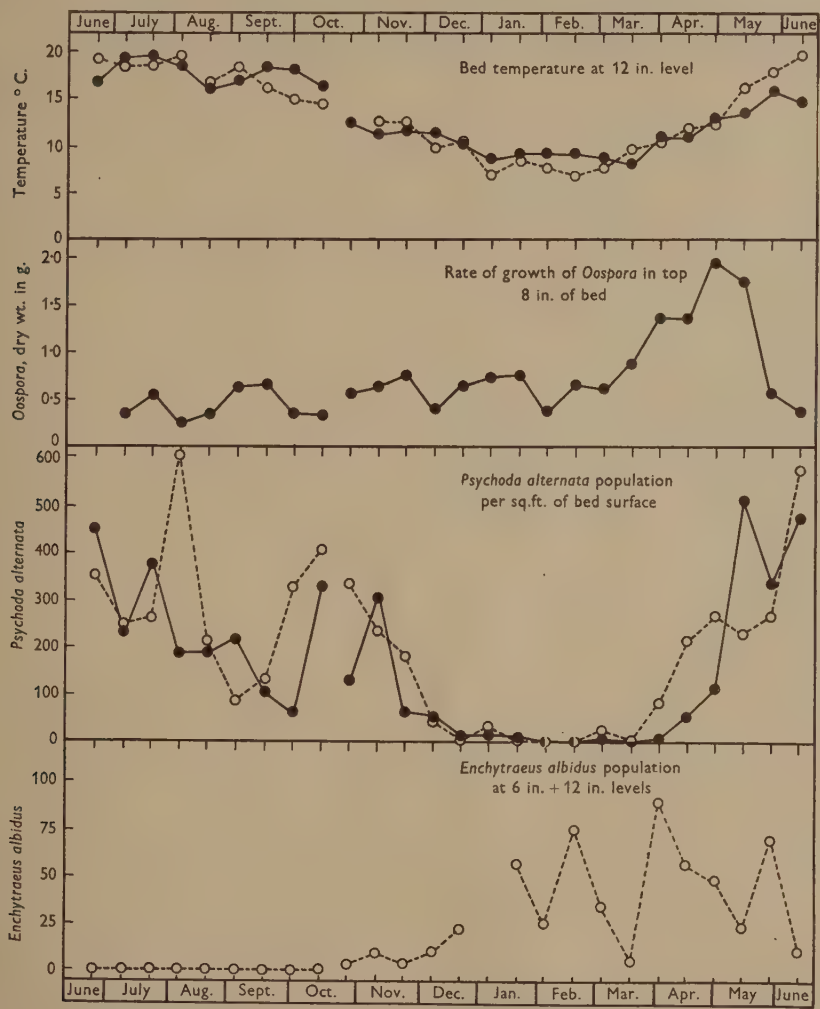


Fig. 3. The bacteria bed community—seasonal fluctuations of bed temperature (°C.), rate of growth of *Oospora* (fungi) in g. per 56 sq.in., *Psychoda alternata* population per sq.ft. of bed surface, and *Enchytraeus albidus* population per sq.ft. at 6 in. + 12 in. levels. Broken line 1939–40, continuous line 1941–2.

with a developmental threshold of 6° C. and a thermal constant of 315° C. (Lloyd *et al.* 1940) was able to progress only very slowly, but the fungus grew relatively quicker (Tomlinson, 1942) and the increase was cumulative. In the early spring, when the bed feeding activities of the rapidly increasing larval population. The fly population in turn was depressed during late August and early September owing to food shortage, and slight recovery of the fungus occurred. Before a second and more complete collapse

of the fly population could occur due to starvation, the differential reaction to temperature during the early winter months began to depress the fly numbers and allowed the fungus to gain; the cycle was then repeated. In this way an oscillation is set up which is dependent partly on climatic and partly on biological factors, supporting the view of Bodenheimer (1938); this depletion of the fungus acts as a partial control of the fly during summer, while low temperature allows the balance to be restored during winter. The fly population starts off each spring from a certain fluctuating threshold of numbers which depends on starvation effects during the preceding summer, losses by washing out, lethal effects of cold (Lloyd *et al.* 1940) and also perhaps from constitutional causes (Bodenheimer, 1938).

The enchytraeid *E. albidus* does not exert an important influence on the fungus-fly relationship. Its population size is largely determined by the activities of the psychodid larvae, which cause the worms to be washed out of the bed in large numbers, particularly during the spring off-loading. Thus the seasonal cycle is a product of winter breeding, when the population is built up, and spring losses, which are not replaced until the next winter. This cycle is also dependent on the down flow of sewage and it is noteworthy that *E. albidus*, which favours terrestrial habitats, suffered much higher proportionate losses in this bed than *Lumbricillus lineatus*, more aquatic in habit, suffered in other beds, suggesting that the latter is better adapted to the bacteria bed. *Enchytraeus albidus* probably owes its presence in the Huddersfield beds to a low temperature threshold of activity, a winter-breeding habit and a high degree of resistance to the chemical sewage; also for these reasons its cycle parallels that of the fungus.

Although corresponding data are not available for the Cooper Bridge beds there is little doubt that similar factors operate to produce similar cycles. Here the more pronounced effects of the toxicity of the Huddersfield sewage towards *E. albidus* will further depress the population. It has been shown (Reynoldson, 1947*b*) that dilution by rain-water may periodically reduce toxicity, but the importance of this is difficult to assess. Also, if *E. albidus* bred mainly during the summer it would combat the effects of toxicity more successfully because of the higher developmental rate of the earlier, more susceptible stages (Reynoldson, 1947*b*), but it would suffer greater losses from larval activity. Some indication of the relative effects of toxicity and larval activity was given by a model bed treating chemical sewage in the laboratory and not harbouring *Psychoda alternata*. Although this sewage is the most toxic of all, it was found that *Enchytraeus albidus* could maintain itself at a steady level in the absence of periodic off-loading induced by the fly larvae. The chemical sewage inhibited the growth of fungus in this bed so that septic conditions such as occurred in the Primary bed were avoided.

A plant-animal relationship of a rather different kind was demonstrated in the Leeds bacteria beds (Reynoldson, 1939*a*). Here fungus is scarce; the dominant plant is a species of the alga *Phormidium* (Cyanophyceae), and being dependent on light it is confined to the surface. The animal concerned is the enchytraeid *Lumbricillus lineatus* while the important abiotic factors are light and temperature. There is no marked seasonal fluctuation in the very large worm population; but during the winter when the bed surface temperature is below 6° C. the worms avoid the surface and are unable to attack the alga. Unlike the fungus the alga cannot progress during the cold season. Quickly following the spring increase in temperature the worms invade and destroy the alga, which largely disappears from the surface. As the light intensity and temperature further increase the alga reforms, and although it is again attacked by the worms it is able to maintain itself until the light intensity begins to wane. An autumn off-loading of the alga may occur. It is clear, therefore, that in these beds the influence of the worm is more transient than that of the larvae and the algal cycle different from that of the fungus in the Huddersfield beds. Factors controlling the growth of the large and stable worm population are obscure but may be the sum total of losses by washing out, winter starvation and the predatory activity of the chironomid larvae (Lloyd *et al.* 1940).

6. SUMMARY

1. The Huddersfield bacteria beds are unusual in harbouring a persistent population of the enchytraeid worm *Enchytraeus albidus* Henle, while the more common *Lumbricillus* (= *Pachydrilus*) *lineatus* Müll. is scarce. This resulted from the inability of *L. lineatus* to tolerate the chemical wastes in the Huddersfield sewage; egg development was totally inhibited and immature and adult stages were also affected. *Enchytraeus albidus* was much more tolerant at all stages of its life cycle, nevertheless, its population was much smaller than that of *Lumbricillus lineatus* in beds treating domestic sewage.

2. Three bed types each offering different environments, due to treating sewages of varying toxicity and at different rates, were studied. Allowing for differences in population age, it is probable that population size was determined mainly by the average toxicity of the sewage. The least favourable bed did not contain any enchytraeids. This was not entirely due to the toxicity of the sewage but also to the secondary development of septic conditions in the absence of an adequate scouring fauna.

3. It is improbable that *L. lineatus* was able to breed in these beds. Comparison of its incidence

with rainfall suggested that it was washed into the beds from natural habitats by flood water.

4. The vertical distribution of *Enchytraeus albidus* was abnormal, showing a maximum concentration below 12 in.; usually enchytraeids live nearer the surface. This was attributed to the higher initial toxicity of the sewage which is gradually reduced by passage through the bed.

5. *E. albidus* showed a marked seasonal cycle with a small summer and higher winter population. The winter maximum was attributed to its habit of breeding most actively during this season and also to smaller losses from washing out. A rapid collapse occurred in the spring due indirectly to the destruction of the fungus *Oospora* (Fungi Imperfecti) by the larvae of the rapidly growing population of flies, *Psychoda alternata* Say. This fungus forms the main food of the worm, and when it is converted to humus by the larvae and washed out of the bed the worms pass out with it. Recovery of the worm is delayed until the autumn when breeding becomes active again. The winter fluctuations in the worm population were also related to periodic off-loading of solids due to *Psychoda* larvae.

6. The bacteria bed community is discussed. Compared with natural habitats it is simple and factors influencing population cycles more easily analysed. At Huddersfield there is a seasonal fluctuation of *Oospora* and *Psychoda alternata* due to differential reaction to temperature. The fungus builds up during the winter when the fly is depressed and is depleted in the spring, by the larvae. The fly population in turn is reduced during late summer due to food shortage. Thus, both climatic and biological factors determine the cycle. *Enchytraeus albidus* plays a minor role in this relationship.

7. ACKNOWLEDGEMENTS

I am indebted to the Department of Scientific and Industrial Research for the Senior Research Award which financed this work. I also wish to thank Prof. E. A. Spaul and Dr Ll. Lloyd for their advice and continuing interest. Dr H. H. Goldthorpe and Dr J. Nixon of the Huddersfield Sewage Works Department have helped in every way, particularly on technical matters and the placing of records at my disposal. The Huddersfield Corporation Authority has also contributed towards the publication costs. Mr E. W. Aubrook, of the Tolson Memorial Museum, Huddersfield, kindly supplied the rainfall data. Finally, I wish to record the assistance of Prof. F. W. Rogers Brambell and my other colleagues of the Zoology Department, University College, Bangor, in the preparation of the paper.

REFERENCES

Allee, W. C. (1931). 'Animal aggregations. A study in general sociology.' Chicago. P. 201.

Backlund, H. O. (1945). 'Wrack fauna of Sweden and Finland: ecology and chorology.' Opusc. Ent. Suppl.: 1–237.

Barritt, N. W. (1931). 'The biological filtration of dilute sucrose solutions.' Biochem. J. 24(2): 1419–46.

Bodenheimer, F. S. (1938). 'Problems of animal ecology.' Oxford.

Fair, G. M. (1934). 'The trickling filter fly (*Psychoda alternata*). Its habits and control.' Sewage Wks. J. 6: 966–81.

Gause, G. F. (1934). 'The struggle for existence.' Baltimore.

Golightly, W. H. (1940). 'Factors influencing the abundance and size of *Psychoda* species in sewage bacteria beds.' Ann. Appl. Biol. 27: 406–21.

Heukelekian, H. (1945). 'The relationship between accumulation, biochemical and biological characteristics of film, and purification capacity of a biofilter and a standard filter. I. Film accumulation.' Sewage Wks. J. 27: 23–38.

Key, A. & Etheridge, W. (1934). 'The oxidation of gas-works liquors in admixture with sewage.' J. Proc. Inst. Sewage Purification, Pt. 1: 134–53.

Lloyd, Ll. (1935). 'The bacteria beds of sewage works as an environment for insects.' Proc. R. Ent. Soc. Lond. 10: 34–9.

Lloyd, Ll. (1943*a*). 'Materials for a study in animal competition. The fauna of the sewage bacteria beds. Part II.' Ann. Appl. Biol. 30: 47–60.

Lloyd, Ll. (1943*b*). 'Materials for a study in animal competition. Part III. The seasonal rhythm of *Psychoda alternata* Say and an effect of intraspecific competition.' Ann. Appl. Biol. 30: 358–64.

Lloyd, Ll., Graham, J. F. & Reynoldson, T. B. (1940). 'Materials for a study in animal competition. The fauna of the sewage bacteria beds.' Ann. Appl. Biol. 27: 122–50.

Moszynski, A. (1930). 'Répartition quantitative des Enchytraeidae dans différents milieux.' Ann. Mus. Zool. Polon. 9: 65–122.

Reynoldson, T. B. (1939*a*). 'Enchytraeid worms and the bacteria bed method of sewage treatment.' Ann. Appl. Biol. 26: 138–64.

Reynoldson, T. B. (1939*b*). 'On the life-history and ecology of *Lumbricillus lineatus* Mull. (Oligochaeta).' Ann. Appl. Biol. 26: 782–99.

Reynoldson, T. B. (1941). 'The biology of the macrofauna of a high-rate, double filtration plant at Huddersfield.' J. Proc. Inst. Sewage Purification: 109–24.

Reynoldson, T. B. (1942). 'Further studies on the biology of a double filtration plant at Huddersfield.' J. Proc. Inst. Sewage Purification: 116–39.

Reynoldson, T. B. (1943). 'A comparative account of the life cycles of *Lumbricillus lineatus* Mull. and *Enchytraeus albidus* Henle in relation to temperature.' Ann. Appl. Biol. 30: 60–6.

Reynoldson, T. B. (1947*a*). 'An ecological study of the Enchytraeid worm population of sewage bacteria beds. Field Investigations.' J. Anim. Ecol. 16: 26–37.

Reynoldson, T. B. (1947*b*). 'An ecological study of the Enchytraeid population of sewage bacteria beds. Laboratory experiments.' Ann. Appl. Biol. 34: 331–45.

Tomlinson, T. G. (1941). 'The treatment of settled sewage in percolating filters in series with periodic change in the order of the filters. Biological Investigations 1938–1941.' J. Proc. Inst. Sewage Purification 39–56.

Tomlinson, T. G. (1942). 'Some aspects of microbiology in the treatment of sewage.' J. Soc. Chem. Ind. Lond. (Trans.) 61: 53–8.

Wishart, J. M. and Wilkinson, R. (1941). 'The purification of settled sewage in percolating filters in series with periodic change in order of the filters.' J. Proc. Inst. Sewage Purification: 15–38.

THE SNOWSHOE RABBIT ENQUIRY, 1943–46

By HELEN CHITTY, *Bureau of Animal Population, Oxford University*

(With 4 Figures in the Text)

1. INTRODUCTION

In 1931–2 the National Parks Bureau of the Canadian Government instituted an enquiry into the population trends of the snowshoe rabbit or varying hare (*Lepus americanus*). Observers were asked whether the species was more abundant, or less abundant, than in the previous year (or had not changed); also whether there had been any epidemics. The enquiry was extended to the U.S.A. and Alaska during subsequent years. Results were analysed at the Bureau of Animal Population and published as shown on p. 44. The war made it impossible to continue the annual papers or to review the past material; and, although the latter task has now been begun, it is not proposed to do more at present than give data similar to those already published.

We are grateful to the Governor and Committee of the Hudson's Bay Company for a grant in aid of this research.

The snowshoe rabbit has a pronounced 9–11-year cycle in numbers over a great part of its range, with corresponding changes in the numbers of its predators such as the lynx (Elton & Nicholson, 1942). Intensive field work on the rabbit cycle has been done, among others, by MacLulich (1937) and by Green and his associates (see, for example, Green & Evans (1940)); but there is no method of following the progress of events in North America as a whole except by an enquiry of the present type. The many objections to the use of subjective data and difficulties of adequately presenting them have been discussed in previous reports (see also below); but a number of clear-cut results justify the questionnaire method.

In the course of 16 years the peaks of two cycles have now been covered. Widespread mortality in 1934–5 was followed by recovery throughout Canada to general abundance which terminated first in Nova Scotia in 1941–2, last in the Yukon as discussed below. In that part of the United States where snowshoe rabbits are known to fluctuate the cycle has followed the same general outline. In Alaska a peak was reached in 1936–7; rabbits then became scarce and had not reached another peak by 1945–6.

2. SOURCES OF INFORMATION

Annual questionnaires were sent out by the National Parks Bureau, Ottawa, the Hudson's Bay Company, Winnipeg and the U.S. Fish and Wildlife Service, Washington, D.C. We wish to thank Dr Harrison F. Lewis, Dr L. Butler and Dr H. H. T. Jackson of these respective organizations for their part in collecting and forwarding the data to Oxford. Observers included the Royal Canadian Mounted Police, post managers of the Hudson's Bay Company, Provincial Game Wardens and the field staffs of the Canadian National Parks. To these and many others we once again extend our thanks.

In addition to the reports summarized below for 1943–6 there were also 54, 38 and 37 others which could not be used. Eighty out of 138 replies received through the Hudson's Bay Company for 1943–4 had been collected on a different system by which the post managers were asked to give the opinions of five trappers instead of their own. Rather than reject this large body of information on the grounds that it is not comparable with previous years, I have used 56 reports where there was a clear majority opinion among the five trappers. The actual division of opinion was as follows: no disagreement (40 reports); 4:1 (16)—all of which were used; 3:2 (16); 1:3:1 (3); 2:2:1 (2); 2:1 (1); 1:1 (2) which were rejected. Nearly all of the disagreement was between 'no change' and one of the other answers: this frequently happens at certain stages of the cycle and at all times in some parts of the country.

3. CANADA

(*a*) 1943–4

In the Yukon the rabbit cycle was still on the upgrade. All but one observer reported increase for 1943–4 and there were statements that rabbits were multiplying rapidly. The area of abundance extended down from the Yukon, including the south-west corner of the North-west Territories, through north-west British Columbia, i.e. west of the main mountain mass. In the southern part of this province, although increase was reported by almost one-third of the observers, nearly two-thirds reported no change. These results confirm our previous conclusions that in this area there has been little apparent difference in numbers of rabbits for many years. During 1943–4 rabbits had 'crashed' in the north-east corner of this province from the Peace River Block northwards.

In the prairie provinces decrease had previously been reported from a belt across the north-central parts; but in 1943–4 the area of decrease also extended

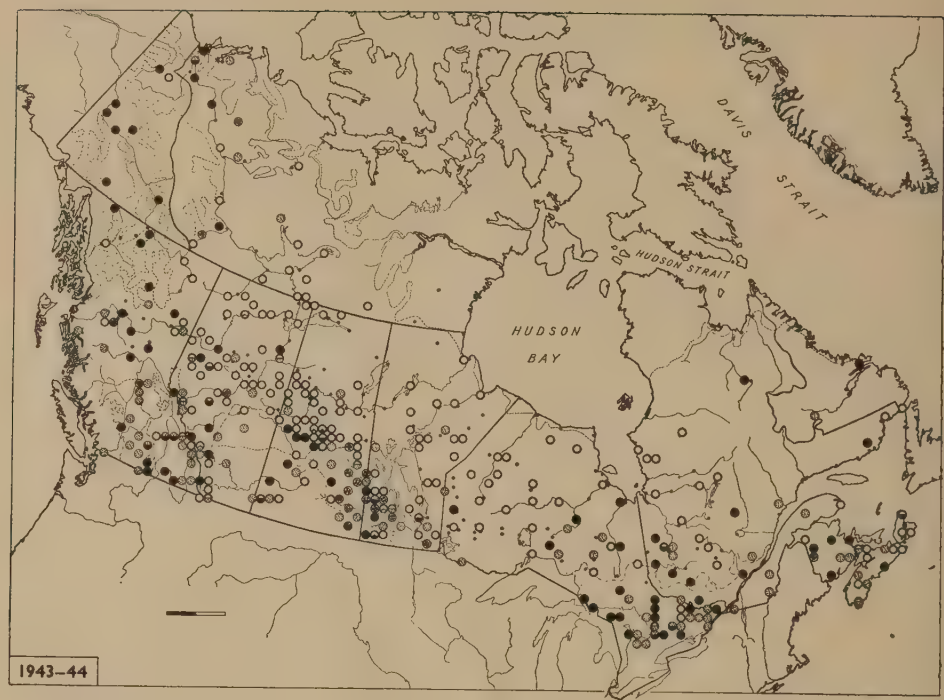
Table 1. *Reports about changes in abundance of snowshoe rabbits in Canada for the years* 1943–4, 1944–5, 1945–6, *each compared with the previous year* (*year ending* 31 *May*)

	No. of observers														
	Increase			Decrease			No change			Total			Epidemic		
	1943–4	1944–5	1945–6	1943–4	1944–5	1945–6	1943–4	1944–5	1945–6	1943–4	1944–5	1945–6	1943–4	1944–5	1945–6
Yukon	8	6	0	1	0	2	0	4	5	9	10	7	0	0	0
North-west Territories	5	7	6	13	13	9	6	6	4	24	26	19	3	1	1
British Columbia	19	8	13	10	12	23	29	38	21	58	58	57	6	1	1
Alberta	9	7	11	54	43	42	22	25	35	85	75	88	6	2	2
Saskatchewan	11	12	9	49	36	23	18	27	21	78	75	53	7	0	1
Manitoba	7	6	8	30	28	18	15	15	4	52	49	30	3	1	0
Ontario	23	21	27	22	27	39	20	36	53	65	84	119	2	0	0
Quebec and Labrador	11	14	10	15	18	27	9	13	11	35	45	48	4	0	0
New Brunswick	4	3	0	2	4	0	4	3	0	10	10	0	0	0	0
Nova Scotia	3	13	17	10	7	7	5	13	8	18	33	32	0	0	0
Total	100	97	101	206	188	190	128	180	162	434	465	453	31	5	5

	% of observers											
	Increase			Decrease			No change			Epidemic		
	1943–4	1944–5	1945–6	1943–4	1944–5	1945–6	1943–4	1944–5	1945–6	1943–4	1944–5	1945–6
Yukon	89	60	0	11	0	29	0	40	71	0	0	0
North-west Territories	21	27	31·5	54	50	47·5	25	23	21	12	4	5
British Columbia	33	14	23	17	21	40	50	65	37	10	2	2
Alberta	11	9	12	63	58	48	26	33	40	7	3	2
Saskatchewan	14	16	17	63	48	43	23	36	40	9	0	2
Manitoba	13	12	27	58	57	60	29	31	13	6	2	0
Ontario	35	25	23	34	32	33	31	43	44	3	0	0
Quebec and Labrador	31	31	21	43	40	56	26	29	23	11	0	0
New Brunswick	40	30	—	20	40	0	40	30	0	0	0	0
Nova Scotia	17	39·4	53	55	21·2	22	28	39·4	25	0	0	0
Total	23	21	22	48	40	42	29	39	36	7	1	1

Table 2. *Reports about changes in abundance of snowshoe rabbits in U.S.A.* (Lepus americanus *only*) *for the years* 1943–4, 1944–5, 1945–6, *each compared with the previous year* (*year ending* 31 *May*)

	No. of observers											
	Increase			Decrease			No change			Total		
State	1943–4	1944–5	1945–6	1943–4	1944–5	1945–6	1943–4	1944–5	1945–6	1943–4	1944–5	1945–6
Maine	1	2	3	0	1	0	4	2	2	5	5	5
Massachusetts	1	1	1	0	0	0	0	0	0	1	1	1
Michigan	3	4	5	3	2	1	9	4	5	15	10	11
Minnesota	1	0	1	0	2	2	0	1	2	1	3	5
New Hampshire	0	0	1	1	0	0	0	1	0	1	1	1
New York	1	1	1	0	0	2	2	2	2	3	3	3
Pennsylvania	0	0	0	0	0	0	0	1	0	0	1	0
Vermont	1	0	2	0	1	0	1	1	0	2	2	2
West Virginia	0	0	0	1	0	0	0	0	1	1	0	1
Wisconsin	3	1	0	0	1	0	0	2	2	3	4	2
Total	11	9	14	5	7	5	16	14	12	32	30	31
Percentage	34	30	45	16	23	16	50	47	39			
Alaska	4	2	1	0	0	0	1	1	2	5	3	3



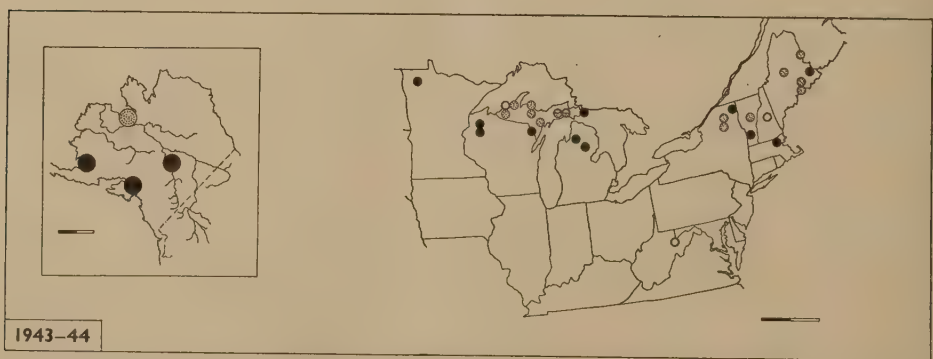


Fig. 1. **1943–44.** Reports about changes in abundance of snowshoe rabbits compared with 1942–43. Each circle of 30 miles diameter (100 miles in Alaska) marks the approximate centre of an area reported on by one or more observers. (For methods see *Canad. Field-Nat.* 54: 117). Increase reports are shown black, decrease white, no change, abundant large irregular dots; all other no change stippled. Where reports at the same centre disagree the circle is divided up in proportion to the number of opinions of each kind. The total length of each scale represents 200 miles.

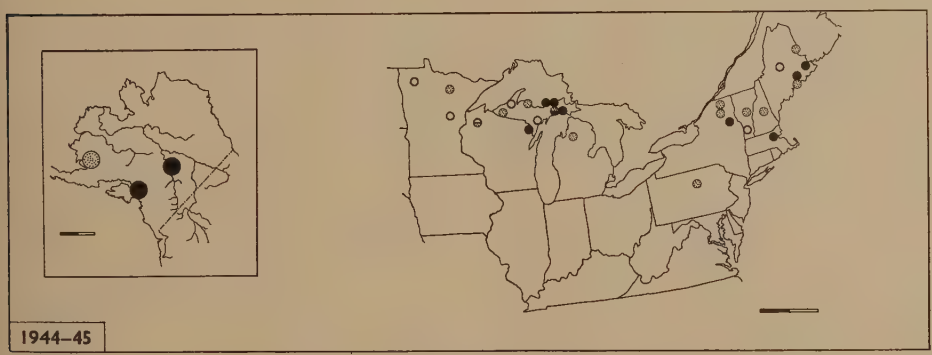


Fig. 2. **1944–45.** Reports about changes in abundance of snowshoe rabbits compared with 1943–44.

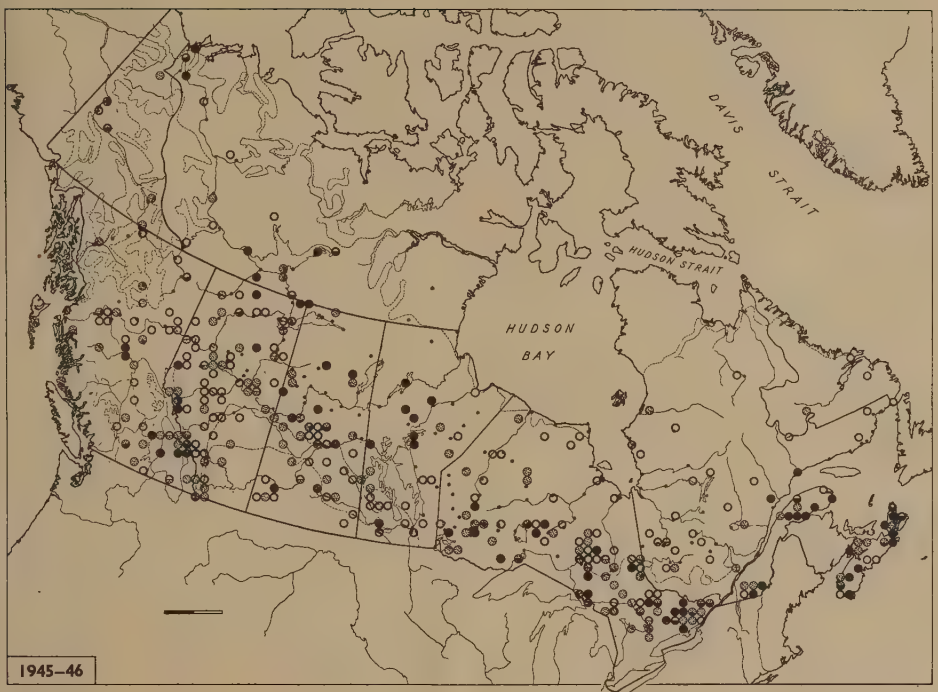


Fig. 3. **1945–46.** Reports about changes in abundance of snowshoe rabbits compared with 1944–45.

northwards to include all of northern Alberta, the area surrounding Great Slave Lake and down the Mackenzie River almost to Fort Good Hope. From north-eastern British Columbia, as noted above, this decrease extended across the prairies and northern Ontario and into northern Quebec around James Bay. South of this belt rabbits had decreased in almost all of Alberta; but increase or abundance was still noted in a small area in the west-central part of the province, throughout most of southern Saskatchewan and in the south-western corner of Manitoba. These areas are south of the main conifer zone.

The Ontario map for 1943–4 shows a most striking change in the relative abundance of snowshoe rabbits. Whereas in 1942–3 the reports were predominantly of increase, the next year decrease was reported from the whole of northern Ontario from the Manitoba border to a line running north-east from Nipigon Bay on Lake Superior to the southern tip of James Bay. There were indications that this condition would be extended farther south in the following season where increase and some signs of abundance were still evident.

In Quebec rabbits were plentiful in the regions contiguous with southern Ontario and in a few other isolated areas. However, the peak of the cycle had evidently been passed over most of the province, as 43 % of the observers reported decrease compared with 17 % during 1942–3.

Rabbits were fairly numerous throughout New Brunswick; but in Nova Scotia they had almost completely disappeared: one observer reported that they had not been so scarce since 1936 and others that only a very few had been seen.

(*b*) 1944–5

The 1944–5 map gives the same general picture as that for the previous year; but there were interesting changes at the two extremes of the Dominion. The area of increase and abundance included only the Yukon and the mouth of the Mackenzie River, rabbits having ceased to increase in most of northern British Columbia. On the other hand, as reports of increase in Nova Scotia had jumped from 17 to 39 %, rabbits were probably beginning to recover in this province. The increase was said to be very slight but definite, and many young rabbits were seen in the spring of 1945. Elsewhere in Canada the situation had altered very little. Rabbits had disappeared from the south-west corner of Manitoba but seemed to be increasing slightly along the Nelson River. They had also disappeared from that part of Quebec adjacent to the Ontario border.

(*c*) 1945–6

The overall picture for 1945–6 was again one of low densities with over 77 % of all observers reporting decrease or 'no change, not abundant'. There were very few major changes from the trends of the previous year. No further increase was reported from the Yukon but rabbits were still plentiful and showed no signs of disease. It is probable that they were at or just past their peak of abundance. The reports of increase from Nova Scotia had risen still more to 53 % so that there is no doubt that the rabbits were on the upgrade of the next cycle. Observers in the Gaspé Peninsula also reported increase but there are insufficient data from previous years to say that this was part of the new cycle. The area of increase apparent in the Nelson River area of Manitoba in 1944–5 had become more firmly established and there were signs of a new focus of increase between Lake Athabaska and Great Slave Lake, and in some areas to the south.

4. UNITED STATES

(*a*) 1943–4

The general picture of increasing abundance revealed by the 1942–3 enquiry was not maintained during 1943–4. The few observers in Minnesota, Wisconsin and the lower peninsula of Michigan still reported increase; but in the upper peninsula of Michigan most observers reported no change and none mentioned abundance. In this area some rabbits were said to be infested with woodticks, and others were noticed to have scabs and blisters. It is likely that 1942–3 or 1943–4 had been the peak year in these states. Rabbits were not plentiful anywhere and were said to be especially scarce in Maine.

(*b*) 1944–5

There was a general scarcity of rabbits during 1944–5 throughout that part of the United States mapped in this enquiry. In Minnesota a sharp decrease was noted and very few were seen in Wisconsin. In the northern peninsula of Michigan some signs of a slight recovery were noticeable, especially in the spring of 1945. There were similar signs of increase in Maine.

(*c*) 1945–6

The increase in northern Michigan was still apparent in 1945–6, although elsewhere in Michigan, Wisconsin and Minnesota rabbits were still very scarce. In the eastern states recovery was well established, 75 % of the observers reporting increase compared with 30 % in 1944–5.

5. ALASKA

During 1943–4 the general recovery reported the previous year for central and eastern Alaska had been maintained, and in the Yukon River Flats rabbits were becoming very abundant. The increase was very slight in the extreme west, around Bristol Bay. On the north-west coast in the drainage areas of the

Unalakleet and Egavik Rivers around Norton Sound rabbits were abundant, although no change was reported. Mr L. V. Palmer writing of this area said: 'Snowshoe rabbits were abundant at Elim (200 miles north of Unalakleet) in 1938–9. They became plentiful in Unalakleet region in 1939–40 and very abundant during 1941, 42 and 43. The trader at Unalakleet states this is the first time in his experience since 1916 that rabbits have appeared in such abundance in this area. Shrub vegetation has increased in the past 25 years.'

the Fairbanks region increase continued and was most noticeable nearest the Yukon border.

6. EPIDEMICS

Disease and mortality in the snowshoe rabbit population was reported by some observers, mostly in Alberta and Saskatchewan, during 1940–1 when the population was still increasing but near its peak. In the following year, 1941–2, when the peak had been reached, there were fewer reports of epidemic, and most of them came from an area in Alberta between

Fig. 4. **1943–44.** Reports of disease and epidemics in snowshoe rabbits. Each circle of 30 miles diameter marks the approximate centre of an area in which dead or dying rabbits were reported by one or two observers.

Increase was again evident in 1944–5 for the Yukon, Tanana and Copper River areas; but for the Bristol Bay area Mr C. M. Carson reported no change and that snowshoe rabbits had been quite scarce since 1936. In his report for the following year, 1945–6, he stated that they were never abundant in this region. The fact that no increase was noted in the rabbit population of the Copper River Valley during 1945–6 was said to have been due to heavy rains throughout the summer. Small increases were apparent nearby in the Kenai Peninsula and in the Susitna Valley. In

the two main areas of the previous year. But, by 1942–3, when the peak had been passed in the prairie provinces the area reporting epidemic had become a wide band across central and southern Alberta and Saskatchewan tapering off across south central Manitoba. By 1943–4, when rabbits were decreasing rapidly, the percentage of observers reporting epidemic in Alberta and Saskatchewan had also decreased but the area from which the reports came was little changed from the previous year. There were, in addition, two reports from northern Ontario (which

had had no epidemic in 1942–3). In 1944–6 there were only five reports of epidemic in each year, all in the western provinces and North-west Territories.

7. SUMMARY

1. Reports have been analysed from 525, 536 and 524 observers in Canada, the United States and Alaska for the years 1943–6.

2. In 1943–4 populations of the snowshoe rabbit or varying hare (*Lepus americanus*) had declined in numbers throughout the Canadian prairie provinces and in Nova Scotia.

3. During the next two years, 1944–6, the area from which low numbers were reported gradually expanded to include almost the whole of the range in Canada and the United States, but not in the Yukon or Alaska. In the Yukon rabbits were still numerous but probably passing their peak; in Alaska the peak had not yet been reached.

4. By the end of the period recovery was well established in the eastern part of the New England states and in Nova Scotia, where the first decreases in the present cycle were reported.

5. Signs of recovery were also noticed in two localities in the prairie provinces and in the upper peninsula of Michigan in 1946–7.

6. The epidemic of 1942–3 rapidly diminished in intensity and did not become widespread outside the western provinces.

7. This report covers the declining phases of the second 9–11-year cycle in numbers since the start of the Snowshoe Rabbit Enquiry and also the beginning of the recovery phases of a third cycle.

REFERENCES

(*a*) *Chronological sequence of previous reports* (*in Canad. Field-Nat.*)

Elton, C. (1933). 'The Canadian Snowshoe Rabbit Enquiry, 1931–32.' 47: 63–9, 84–6.

Elton, C. (1934). 'The Canadian Snowshoe Rabbit Enquiry, 1932–33.' 48: 73–8.

Elton, C. & Swynnerton, G. (1935). 'The Canadian Snowshoe Rabbit Enquiry, 1933–34.' 49: 79–85.

Elton, C. & Swynnerton, G. (1936). 'The Canadian Snowshoe Rabbit Inquiry, 1934–35.' 50: 71–81.

Chitty, D. H. & Elton, C. (1937). 'The Snowshoe Rabbit Enquiry 1935–36.' 51: 63–73.

Chitty, D. & Elton, C. (1938). 'The Snowshoe Rabbit Enquiry 1936–37.' 52: 63–72.

Chitty, D. & Elton, C. (1939). 'The Snowshoe Rabbit Enquiry 1937–38.' 53: 63–70.

Chitty, D. & Elton, C. (1940). 'The Snowshoe Rabbit Enquiry 1938–39.' 54: 117–24.

Chitty, D. & Chitty, H. (1942). 'The Snowshoe Rabbit Enquiry, 1939–40.' 56: 17–21.

Chitty, D. & Nicholson, M. (1943). 'The Snowshoe Rabbit Enquiry, 1940–41.' 57: 64–8.

Chitty, H. (1943). 'The Snowshoe Rabbit Enquiry, 1941–42.' 57: 136–41.

Chitty, H. (1946). 'The Snowshoe Rabbit Enquiry, 1942–43.' 60: 67–70.

(*b*) *Other references*

Elton, C. & Nicholson, M. (1942). 'The ten-year cycle in numbers of the lynx in Canada.' J. Anim. Ecol. 11: 215–44.

Green, R. G. & Evans, C. A. (1940). 'Studies on a population cycle of snowshoe hares on the Lake Alexander area. III. Effect of reproduction and mortality of young hares on the cycle.' J. Wildlife Manag. 4: 347–58.

MacLulich, D. A. (1937). 'Fluctuations in the numbers of the varying hare (*Lepus americanus*).' Univ. Toronto Stud., Biol. Ser. No. 43: 1–136.

THE SIGNIFICANCE OF LITTER-SIZE

By DAVID LACK, *Edward Grey Institute of Field Ornithology, Oxford*

1. INTRODUCTION

This paper is purely introductory and speculative. Its object is to draw attention to an unexplored field problem in mammals in which the writer became interested through his parallel studies on clutch-size in birds (Lack, 1947, 1948). Within certain limits, litter-size is characteristic for each species of mammal, but the ecological significance of this fact seems to have been largely misunderstood, partly because litter-size has been studied mainly by physiologists, not ecologists, and partly owing to a popular fallacy regarding the nature of population balance.

By litter-size is here meant the number of young at birth. The potential litter-size before birth is also of great interest, but is outside the scope of this paper. However, as ecologists and others have sometimes used different criteria for estimating litter-size (e.g. when comparing the average litter-size of the same species in different regions), it should be emphasized that losses occur at every stage, so that the average number of ova ovulated, ova implanted, embryos *in utero* at an early stage, embryos at a late stage, young at birth and young at weaning, are not necessarily the same.

2. LITTER-SIZE AND NATURAL SELECTION

Litter-size has hitherto been studied mainly in domestic animals, often with the practical aim of increasing fecundity. It is, therefore, not surprising that the emphasis of research has been mainly on the physiological factors involved, and not on the selective value of litter-size in wild populations. As a result, it has sometimes been assumed that physiological factors are all-important, and that a mammal has as many young as it is physiologically capable of producing. In one sense the latter statement is a truism, but it cannot be the whole explanation. Distinction must be made between the proximate factors concerned with internal physiology and the ultimate factors concerned with survival value.

Litter-size is known to be influenced by hereditary factors. For instance, the wild pig (*Sus scrofa*) has an average litter of 4, but domestic breeds have varying numbers up to 12 (Asdell, 1946). The wild rabbit (*Oryctolagus cuniculus*) usually has 4–5 young (in England), but the small Polish breed averages 3·2 per litter, the Flemish Giant 10·2 per litter, and the hybrid between them 7·8 per litter (Gregory, 1932; Hammond, 1941). Similar data are available for other species, also for man (Greulich, 1934). As domestic breeds of rabbit, pig and others have larger litters than the wild forms, mutations resulting in larger litters must be eliminated from the wild populations by natural selection. This paper is primarily concerned with the possible grounds on which such selection operates.

The popular view, repeated in explicit or implicit form in many text-books, is that the reproductive rate of each species has been adjusted by natural selection so as to equal the total mortality, thus keeping the population balanced. It is claimed that such an arrangement has survival value through preventing over-population. For instance, it is claimed that if an elephant produced more than one young at a birth, the population would multiply excessively, to the detriment of the species. In the writer's opinion, this view is fallacious, first because natural selection does not work in the manner postulated, and secondly because it would not usually result in population balance.

Considering the first objection, natural selection works for the survival of certain types of individuals, and not necessarily 'for the good of the species'. Suppose, for instance, that a mutation appears by which an elephant has two instead of one young at a birth. If other things are equal, this mutation will spread through the population, since the individuals possessing it will leave twice as many offspring as the others, and such spread will occur even if it results in over-population. A parallel argument applies to all other species. The only way in which a mutation for increased litter-size can be checked is if it carries with it some disadvantage to the individuals possessing it and/or to their offspring, so that these individuals have fewer descendants than those producing litters of smaller size.

Secondly, while it is true that, in a balanced population, birth-rate and mortality must be equal, the correct inference from this is almost the reverse of the popular one. An animal population can remain balanced only if it is in dynamic, not static, equilibrium. This means that, when the population density rises above the average, there are factors which tend to reduce it, and when it falls below the average, there are factors which tend to raise it. Moreover, the further the departure from the average density, the stronger the intensity with which these factors work (Nicholson, 1933). Theoretically, litter-size could be such a controlling factor, but only if it

decreased markedly as the population density rose, and increased markedly as the population density fell. The available field data, though inadequate, strongly suggest that litter-size does not vary sufficiently, nor in such directions as, to achieve such a balance. While much more research is needed, it is far more probable that mammal populations are primarily controlled by mortality factors whose intensity varies with the population density. While it remains true that, in a balanced population, birth-rate and mortality are equal, such correspondence is primarily brought about by variations in the mortality and not the birth-rate.

The only other tenable hypothesis is that litter-size is selected *per se*, and that the genotypes selected are those which result in the maximum number of descendants. It is easy to see why genotypes with unusually small litters should give rise to fewer descendants than those with litters of average size, and hence why the former should tend to be eliminated from the population. The interesting point is to determine why genotypes with litters of unusually large size should produce fewer descendants than those with litters of average size. The working hypothesis adopted by the writer for birds, and here applied to mammals, is that the upper limit is set by the number of young which the parents can successfully raise; that, as litter-size increases, the proportionate mortality among the young increases, and that eventually an optimum litter-size is reached, beyond which the initial advantage of an extra youngster is more than offset by the rise in proportionate mortality. Field data on this problem are not yet available for any wild population of mammals, but there are suggestive data for certain domestic and laboratory stocks.

3. THE LABORATORY GUINEA-PIG

Wright & Eaton (1929), who were primarily concerned with other problems, provide valuable and extensive data on survival in relation to litter-size in a laboratory population of the guinea-pig (*Cavia porcellus*). The data for their control stock and for two of their inbred families are set out in Table 1. They obtained similar data for their other inbred strains, not reproduced here.

The data in Table 1 show clearly that, excluding litters of 1, the proportionate mortality among the young rises as litter-size increases. This holds both for the proportion of still-births and for the proportion of young which die between birth and weaning at 33 days. The average productivity of each litter-size (item (5) in the table) is obtained by multiplying the proportion of surviving young by the initial number in the litter. This shows that, in the control stock, maximum productivity at weaning is attained with a litter of 5, from which an average of 2·7 young are weaned. With a litter of 6, productivity falls to only 1·8 young weaned per litter, due to the marked increase in proportionate mortality. Similarly, in inbred family 2, maximum productivity is attained with a litter of 4, and in inbred family 13 with a litter of 3. (In general, the inbred strains are less successful than the control stock, a problem which need not be discussed here.) The other inbred strains provide very similar data, and in each case maximum productivity is attained with a litter of between 3 and 5 young, i.e. at a litter-size below the maximum observed in the stock.

The above data therefore support the general principle announced at the end of the previous section. Owing to the rise in proportionate mortality, the most productive litter-size is not the largest. However, there is an apparent discrepancy. In the control stock, the most productive litter-size is 5, but the commonest litter-size is not 5 but 3. Likewise, in family 2, 4 is the most productive but 2 is the commonest litter-size. In the other inbred families, not reproduced in Table 1, the commonest litter-size also tends to be smaller than the most productive litter-size, and family 13 (in Table 1) is exceptional in that 3 is both the most productive and the commonest (only just) litter-size. Note that the litter-size which was commonest was never larger than that which was the most productive.

The above discrepancy can reasonably be attributed to four factors. First, the data in Table 1 stop at weaning. For a complete estimate of productivity, subsequent survival must also be included. Item (8) in Table 1 shows that the average weight of the young at weaning is markedly lower when litter-size is larger. A lower weight at weaning might adversely affect the chances of subsequent survival, thus further handicapping the young from large as compared with small litters.

Secondly, the data refer to laboratory conditions. In the wild, the post-natal mortality would almost certainly be higher, and it is reasonable to suppose that this additional mortality would be proportionately heavier in large than small litters. The most productive litter-size in the wild is therefore likely to be rather smaller than the most productive litter-size in the laboratory. Hence one might also expect the commonest litter-size in the wild to be smaller than the most productive in the laboratory. (This effect will be counteracted by any artificial selection for higher litter-size in the laboratory stock, but such selection has probably not yet continued for very long.)

Thirdly, Wright & Eaton state that a litter of small size to some extent indicates unfavourable conditions. The physiological factors involved in this modification are outside the scope of the present paper, but the fact that litter-size can be modified adaptively is highly relevant. If such an adaptation were perfect, and litter-size could always be adjusted to suit the

conditions, then a litter of large size would be produced only when it was the most productive; then, data like those in Table 1 would show that the most productive litter-size was the largest. In fact, the latter is not the case, indeed one could hardly expect such an extreme condition to hold. Also, Wright & Eaton state that only some of the litters of small size were attributable to phenotypic variation. For a complete analysis of the effect of natural selection on litter-size, adaptive modifications must be separated from genotypic differences, which cannot at present be done. The unavoidable inclusion in Table 1 of a proportion of adaptive variations in litter-size means that the survival from litters of small size is rather lower, and that from litters of large size is rather higher, than would have been the case had all the differences been genotypic.

Fourthly, the essential figure is the productivity per parent rather than the productivity per litter. The production of larger litters possibly reduces the chances of survival of the parent, and hence her total productivity. This factor may well be of minor or no importance.

To conclude, the data in Table 1 do not conflict essentially with the view that litter-size has been selected through optimum productivity, and the fact that the commonest litter-size is rather smaller than the most productive is explicable because (*a*) mortality after weaning has not been allowed for, (*b*) laboratory conditions are more favourable to survival than natural conditions, (*c*) some, but not all, of the differences in litter-size are adaptive modifications, (*d*) the production of larger litters possibly reduces the breeding life of the parent.

Table 1. *Survival according to litter-size in the laboratory guinea-pig*

(After Wright & Eaton, 1929)

Litter-size	1	2	3	4	5	6
A. The Control Stock						
(1) No. of litters studied	159	322	367	189	51	16
(2) % of young born alive	81	90	87	80	81	62
(3) % of live births raised to 33 days	84	87	84	78	68	49
(4) % of all young (born alive or dead) raised to weaning (33 days)	68	78	73	62	55	30
(5) Av. no. raised per litter to 33 days	0·7	1·6	2·2	2·5	2·7	1·8
(6) Av. birth-weight (g.)	110	91	77	67	59	53
(7) Av. daily gain in wt. (g.) to 33 days	5·9	5·1	4·2	3·9	3·5	3·6
(8) Av. wt. (g.) at weaning (33 days)	310	264	219	201	181	177
B. Inbred Family 2						
(1) No. of litters studied	166	438	348	106	9	—
(2) % of young born alive	68	82	83	80	58	—
(3) % of live births raised to 33 days	83	85	85	80	58	—
(4) % of all young (born alive or dead) raised to weaning (33 days)	56	70	71	64	33	—
(5) Av. no. raised per litter to 33 days	0·6	1·4	2·1	2·6	1·7	—
(6) Av. birth-weight (g.)	88	76	65	58	51	—
(7) Av. daily gain in wt. (g.) to 33 days	3·6	3·5	3·1	2·8	2·8	—
(8) Av. wt. (g.) at weaning (33 days)	213	195	172	155	154	—
C. Inbred Family 13						
(1) No. of litters studied	141	324	325	172	48	11
(2) % of young born alive	85	82	79	65	53	36
(3) % of live births raised to 33 days	78	82	78	66	60	33
(4) % of all young (born alive or dead) raised to weaning (33 days)	67	67	62	43	31	12
(5) Av. no. raised per litter to 33 days	0·7	1·3	1·9	1·7	1·6	0·7
(6) Av. birth-weight (g.)	110	89	75	63	55	50
(7) Av. daily gain in wt. (g.) to 33 days	5·5	5·1	4·4	4·0	3·6	4·7
(8) Av. wt. (g.) at weaning (33 days)	300	264	227	204	186	217

Note. The litters with more than six young were omitted from the table as they were too few to yield significant results.

4. DATA ON OTHER SPECIES

There seem to be few relevant data on other species. Those that exist demonstrate an increase in proportionate mortality with increasing litter-size, but in most cases they are not sufficiently complete to show the turning point, at which a further increase in litter-size is more than offset by the increase in mortality among the young.

In the horse (*Equus caballus*), single births are the rule; twins are rare. Data summarized by Hammond (1941) and Asdell (1946) for various domestic breeds show that the proportion of still-births is far higher among twin than single births. A similar state of affairs holds in cattle (*Bos taurus*) (Strandskov & Ondina, 1947, quoting Johansson, 1932). In horses and cattle, the percentage of still-births among twins does not usually exceed 50%, so that twins are apparently more productive than single births, but these data take no account of post-natal mortality, which might also be expected to be higher in twins than single young. Hence the data do not necessarily conflict with the view that the commonest litter-size, in this case 1, is also the most productive.

Data on the coypu (*Myocastor coypus*) have been obtained on Russian fur-farms by Vereshchagin (1941), and are set out in Table 2. The averages are rather erratic, suggesting that the number of litters studied was small. They show a rise in the proportion of still-births with increasing litter-size, and maximum productivity is apparently reached with a litter of 8, whereas the average litter-size in the wild is said to be between 4 and 5. However, these two results are not necessarily discordant, as the data refer solely to still-births, and post-natal mortality has not been included.

Table 2. *Mortality at birth in the coypu*
(After Vereshchagin, 1941)

Litter-size	% born alive	Productivity per litter
1	100	1·0
2	89	1·7
3	94	2·8
4	93	3·7
5	86	4·3
6	84	5·0
7	72	5·0
8	69	5·5
9	45	4·0
10	50	5·0
12	0	0

Likewise in man (*Homo sapiens*), the proportionate mortality is greater in multiple than single births (Strandskov & Ondina, 1947). In man, the proportion of still-births is not, by itself, nearly sufficient to account for single births being the most favoured number. However, the studied population was living under highly favourable conditions, and no allowance has been made either for post-natal mortality or for the possible effects of multiple births on the survival of the mother. In man, unlike other mammals, selection for family size is further complicated by the fact that the young from different births associate together in one family.*

Table 3. *Still-births in Man (white and coloured U.S. population)*
(After Strandskov & Ondina, 1947)

No. at a birth	% still-births	Productivity per litter
Single births	3·5	1·0
Twins	7·5	1·9
Triplets	14·3	2·6
Quadruplets	19·9	3·2

5. ADAPTIVE MODIFICATIONS

As mentioned already, Wright & Eaton found evidence of adaptive modifications in litter-size. There is also field evidence for phenotypic variations in litter-size, though whether they are also adaptive is in most cases speculative. For instance, litter-size may vary with the season of the year, as shown for *Microtus* by Hamilton (1937), and for many other species quoted by Asdell (1946), including common hare (*Lepus europaeus*), common shrew (*Sorex araneus*), rat (*Rattus norvegicus*), mouse (*Mus musculus*), guinea-pig, fox (*Vulpes*), sheep (*Ovis aries*), and pig. In some species the seasonal variation is small, in others large. In the common hare, for instance, the spring litters may be twice the size of the winter ones. It seems reasonable to suppose that such seasonal variations are adaptive, the larger litters being produced at those seasons which are more suitable for raising young.

In *Microtus*, Hamilton (1937) also found a marked difference in litter-size between one year and another. The average for July in three years during which the population was increasing was 6·0, 6·0 and 6·2 respectively, while in a 'crash' year it was only 4·5. MacLulich (1937) quotes writers who consider that there is a similar annual variation in the litter-size of the varying hare (*Lepus americanus*), though he himself found little evidence of it. Again, Braestrup (1941) has suggestive evidence that, in inland populations of the arctic fox (*Alopex lagopus*), which feed primarily on lemmings (*Dicrostonyx groenlandicus*), the average litter-size is much higher in years when lemmings are

* The Dionne quintuplets present a new and rather charming complication, as the care and money expended on their nurture might now mean that, in the New World, the chances of post-natal survival are higher for quintuplets than for single births. This tendency would, of course, hold only so long as quintuplets were extremely rare.

abundant than in years when they are scarce. On the other hand, in coastal populations of the arctic fox, which feed primarily on marine organisms, average litter-size shows little annual variation, and is only about half the litter-size found among inland fox populations during a peak lemming year.

Clear evidence that food can influence litter-size is given by Bittner (1936, quoted by Grüneberg, 1943); when a laboratory population of mice was fed on fox chow instead of rolled oats, average litter-size rose from 4·8 to 5·7.

Litter-size also varies with the age of the parent, usually being smaller in very young and very old parents than in those of intervening age. This has been shown for the laboratory rat by King (1939), for captive voles (*Microtus agrestis*) by Leslie & Ranson (1940), for the laboratory mouse by Grüneberg (1943) and for many other species quoted by Hammond (1941) and Asdell (1946), including fox, sheep, pig, cattle and rice-rat (*Oryzomys palustris*). Usually, this age variation seems to have been interpreted solely in physiological terms. Physiological factors of course bring it about, but it may reasonably be suggested that natural selection has been the ultimate factor concerned, due to the fact that, among very young and very old parents, the most productive litter-size tends to be rather smaller than it is in parents in the prime of life.

The above, and other, phenotypic modifications may be adapted to changes in either the post-natal or the pre-natal conditions, and for a complete analysis the latter must be studied as well as the former. To cite one possible situation, Wright & Eaton's data show that a larger litter involves a smaller weight at birth, and the latter probably involves a reduced chance of subsequent survival. If feeding conditions were unusually favourable, it might be physiologically possible for a female rodent to utilize the additional nourishment by producing either the normal number of young at a heavier birth-weight, or more young at the normal birth-weight. Either alternative might result in a higher productivity and if, as might well be the case, the latter alternative had a higher productivity than the former, then natural selection would favour the evolution of a capacity to modify litter-size with food supply. However, while this evolution would be brought about through differences in post-natal survival, the basic factor concerned would be the influence of food on pre-natal conditions, through the effect of the latter on birth-weight. A parallel argument might account for the fact that, within a given species, parents of larger body-size tend to have larger litters, of which many examples are cited by Hammond (1941) and Asdell (1946). Clearly, post-natal and pre-natal factors are closely linked, and cannot be dissociated in an adequate analysis, but the discussion of pre-natal factors is omitted here, first because they do not affect the basic hypothesis, secondly because many additional complications are introduced, and thirdly because the author is incompetent to discuss them.

6. CONCLUSION

For the field naturalist, the next stage should be a more detailed study than has yet been made of the intraspecific, regional, seasonal and other variations in litter-size which occur in nature, and above all a study in a wild mammal population of post-natal survival in relation to litter-size. The latter is much more difficult than in birds, where the young are at first confined to a nest and can later be traced with numbered rings, but it should not be insuperable.

Three difficulties in such a study may be particularly stressed. First, the study should be continued for more than one season, as there may well be marked differences in survival in relation to litter-size in different years. Secondly, owing to the existence of adaptive modifications, the litter-size which is most productive will not necessarily be that which occurs most frequently. Indeed the difference between the most frequent and most productive litter-size will provide some indication of the extent of adaptive modification in the species concerned. Thirdly, as natural selection will be particularly severe on characters affecting reproductive rate, hereditary differences resulting in litter-sizes above or below those at which maximum productivity occurs will be very rare. Hence, while one should be able to demonstrate the rise in proportionate mortality with increasing litter-size, it is unlikely under natural conditions that one will have enough material to demonstrate the point at which a further increase in litter-size causes a fall in productivity.

It will also be of great interest to pursue the present argument in other groups of organisms. Where there is no parental care, the problem is probably simpler, but, here also, reproductive rate may be expected to be limited by the rise in proportionate mortality with an increasing number of offspring, though the factors causing this mortality may be very different in different groups. Again, too, one may expect to find adaptive modifications to different conditions. To cite only two cases out of many, Turner (1938) showed that, in the ovoviviparous poecilid fish *Brachyrhaphis episcopi*, the number of young in a brood depends greatly on the body-size of the parent, the smaller the parent the smaller the average number of young. Again, it is known for various insects that the number of eggs laid falls if the organisms are crowded, and Maclagan (1932) has shown that, at least in one case, this is primarily due to a shortage of food not to crowding as such.

Finally, this paper has been concerned solely with the limitation of litter-size within the conditions of

a single species. Additional controlling factors become apparent when different species are compared, and when a long-term evolutionary standpoint is adopted, as already shown for birds (Lack, 1948). In all groups of animals and plants, there is the evolutionary alternative between producing more young, or fewer young which are better nourished and better protected. In all cases, natural selection may be expected to work towards maximum productivity, but the latter will be achieved in very different ways in different cases, depending on the environments to which the offspring are exposed.

7. SUMMARY

1. An explanation of litter-size purely in terms of physiological capacity is inadequate. Ultimately, litter-size depends on hereditary factors and is subject to natural selection.

2. It is fallacious to suppose that litter-size has been adjusted by natural selection so as to balance the annual mortality of the species.

3. Selection must favour those genotypes which give rise to the maximum number of new parents. Within a species the upper limit of litter-size is thought to be determined by the increase in proportionate mortality among the young with increasing litter-size, so that eventually a point is reached beyond which an increase in the initial number of young is more than offset by the greater mortality.

4. The above principle is illustrated by Wright & Eaton's data on survival in laboratory guinea-pigs. Reasons are given as to why the most frequent litter-size should be rather smaller than that which apparently has the highest productivity.

5. Litter-size can be modified adaptively. The existence of such modifications will usually mean that, in a wild state, as in the laboratory, the most productive litter-size is rather larger than that most frequently found.

6. Post-natal and pre-natal factors are closely linked, particularly in regard to adaptive modifications, but pre-natal factors are not further considered here.

8. ACKNOWLEDGEMENTS

Being outside my special field of knowledge, this paper has come in for particularly stringent criticism before publication, and I am most grateful to Professor Rogers Brambell, C. S. Elton, P. H. T. Hartley and H. N. Southern for the trouble they took in supplying it; also to Prof. Sewall Wright and Prof. H. H. Strandskov of the University of Chicago for drawing my attention to the mammalian parallels with my work on birds.

REFERENCES

Asdell, S. A. (1946). 'Patterns of mammalian reproduction.' Ithaca, New York.

Bittner, J. J. (1936). 'Differences observed in an inbred albino strain of mice following a change in diet. 1. Litter-size.' Nutr. Bull. No. 1 Jackson Mem. Lab., Bar Harbor Maine, pp. 3–9. (Quoted by Grüneberg, 1943, and not seen by the present writer.)

Braestrup, F. W. (1941). 'A study on the arctic fox in Greenland: immigrations, fluctuations in numbers: based mainly on trading statistics.' Medd. om Grønland, 131 (No. 4): 1–101 [pp. 13–16].

Gregory, P. W. (1932). 'The potential and actual fecundity of some breeds of rabbits.' J. Exp. Zool. 62: 271–85.

Greulich, W. W. (1934). 'Heredity in human twinning.' Amer. J. Phys. Anthrop. 19: 391–431.

Grüneberg, H. (1943). 'The genetics of the mouse.' Cambridge.

Hamilton, W. J. (1937). 'The biology of microtine cycles.' J. Agric. Res. (Wash.) 54: 779–90.

Hammond, J. (1941). 'Fertility in mammals and birds.' Biol. Rev. 16: 165–90.

Johansson, I. (1932). 'The sex ratio and multiple births in cattle.' Zeitschr. f. Zuchtung b. Tiersuchtung 24: 183–286. (Quoted by Strandskov and Ondina, 1947; not seen by the present writer.)

King, H. D. (1939). 'Life processes in gray Norway rats during fourteen years in captivity.' Amer. Anat. Memoirs No. 17: 1–77 [esp. pp. 32–7].

Lack, D. (1947, 1948). 'The significance of clutch-size.' Ibis, 89: 302–52; 90: 25–45.

Leslie, P. H. & Ranson, R. M. (1940). 'The mortality, fertility and rate of natural increase of the vole (*Microtus agrestis*) as observed in the laboratory.' J. Anim. Ecol. 9: 27–52.

Maclagan, D. S. (1932). 'The effect of population density upon rate of reproduction with special reference to insects.' Proc. Roy. Soc. B, 111: 437–54.

MacLulich, D. A. (1937). 'Fluctuations in the numbers of the varying hare (*Lepus americanus*).' Univ. Toronto Studies Biol. Ser. 43: 1–136 [esp. pp. 90–1].

Nicholson, A. J. (1933). 'The balance of animal populations.' J. Anim. Ecol. 2: 132–78.

Strandskov, H. H. & Ondina, D. (1947). 'A comparison of the percentages of still-births among single and plural births in the total, the "White" and the "Colored" U.S. populations.' Amer. J. Phys. Anthrop. N.S. 5: 41–54.

Turner, C. L. (1938). 'The reproductive cycle of *Brachyraphis* [recte *Brachyrhaphis*] *episcopi*, an ovoviviparous Poeciliid fish, in the natural tropical habitat.' Biol. Bull. 75: 56–65.

Vereshchagin, N. K. (1941). ['Establishment of the nutria (*Myocastor coypus* Mol.) in west Georgia.'] Trav. Inst. Zool. Acad. Sci. R.S.S.G. 4: 3–42. (Read in translation from Russian by J. D. Jackson in Bureau of Animal Population.)

Wright, S. & Eaton, O. N. (1929). 'The persistance of differentiation among inbred families of guinea pigs.' U.S. Dept. Agric. Tech. Bull. 103: 1–45.

THE FAUNA OF FOUR STREAMS IN THE 'BLACK MOUNTAIN' DISTRICT OF SOUTH WALES

By J. R. ERICHSEN JONES
Department of Zoology, University College of Wales, Aberystwyth

(With 3 Figures in the Text)

CONTENTS

	PAGE
1. Introduction	51
2. The environment	51
(*a*) General topography	51
(*b*) General descriptions of the streams studied, collecting stations, macroflora	52
(*c*) Chemical	54
(*d*) Gradient and current speed	55
(*e*) Temperature	56
3. The fauna	56
(*a*) Collecting methods	56
(*b*) The species recorded	58
(*c*) Remarks on the fauna	58
4. Summary	64
References	64

1. INTRODUCTION

The general ecology of running waters has not been greatly studied in this country, and of recent years investigations have tended to take the form of specialized study of particular animal groups, like the work of Puri (1925) and Smart (1944) on the Simuliidae. The metallic pollution prevalent in north Cardiganshire, as a result of the lead mining carried on in the nineteenth century, has been a considerable stimulus to study of the fauna and general ecology of the rivers and streams of west Wales. The work was begun by Carpenter (1924), who studied first the rivers Rheidol and Ystwyth, and later (1927) dealt with the faunistic ecology of Cardiganshire streams, including those of the high Plynlimmon plateau, on the lines of a broad survey. This study, however, does not give a complete picture of the fauna of any particular stream and the only detailed descriptions of the fauna of Welsh mountain streams are to be found in my paper (1941) on the River Dovey, in which 57 species are recorded for the main stream above the 400 ft. contour, and my paper (1943) on the River Teifi; here about 60 species are recorded for the upper portion of the river from its source to the Tregaron Bog (500 ft.). In the summer of 1947 the writer was presented with an opportunity to make a study of the streams in the Black Mountain district of south Wales. When the work was begun it was anticipated that the many streams of the area would prove to have a general similarity of environmental features, fauna and flora, and that a detailed survey of one could be taken as representative. A preliminary reconnaissance was sufficient to show that this was not the case. Four streams were eventually selected for systematic study. Three run on the southern slopes—the upper reaches of the River Amman and its main tributaries the Nant Garw and Nant Pedol, and one on the northern slopes—the River Clydach.

2. THE ENVIRONMENT

(*a*) *General topography*

The Black Mountain, about 15 miles north of Swansea Bay and on the borders of the south Wales coal basin, forms the western end of a 40-mile range running west to east between Llandilo and Abergavenny and separated from the hills of central Wales by the valley of the River Usk. The broad central portion of this range is marked on Ordnance maps as Fforest-fawr, and in the east the mountains rise to nearly 3000 ft. at the Brecon Beacons. The Black Mountain probably derives its name from the broad expanses of dark, broken rock on its southern slopes, and is not to be confused with the Black Mountains, which lie to the east of Brecon. Above 1000 ft. the land is uncultivated and uninhabited, completely treeless except for an occasional stunted hawthorn. The soil is thin and for the most part the vegetation is rough and yellowish mountain pasture with moss in damp situations, but in the extreme west this is partly replaced by ferns, heather and bilberries. On the whole the climate is equable (mean January and July temperatures 40 and 61° F.) and snowfalls are hardly more frequent than in the valleys below, though when snow is deposited it may lie for considerable periods

in winter. The prevailing winds are west and south-west, and bring much rain, the mean annual rainfall being 50–80 in. for the greater part of the area and over 80 in. at high altitudes. Consequently streams are numerous and swift, carrying very little suspended matter even in full flood.

(*b*) *General descriptions of the streams studied, collecting stations, macroflora*

The River Amman has its source in peaty soil at an altitude of about 1700 ft. It is probable that this soil is highly acid, for small black-bottomed pools near the source of the river, but not directly connected with it, have very acid water (pH 4·0–4·2) and the water of the river is always acid, particularly at flood-time. Near its source the stream is too inaccessible for regular study and all fauna samples were taken between the points marked *A* in Fig. 1. Here the valley is open, with no tree shade. The stream-bed is 10–15 ft. wide and somewhat irregular in gradient, in some places formed of smooth, pot-holed rock, in other places strewn with stones of all sizes from large boulders to pebbles. Small pools are common, but these are all directly in the path of the flowing water and bottomed with large stones. Frequent violent floods sweep away all mud, but in the shelter of large boulders a little sand and gravel may be deposited. The flora appears scanty, clods fallen in from the banks may bear tufts of grass in which beetles shelter and a little liverwort, *Aplozia riparia*, grows on some of the larger stones, but no other bryophytes were seen and except for quantities of *Batrachospermum* algal growth does not appear abundant. At some points the flora is so lacking, and the irregular, craggy stones of the stream-bed are so clean and so little weathered that the stream hardly has the appearance of a permanent water-course. At normal level the water is very clear and faintly yellow; in full flood the peat-yellow colour is much intensified but the water remains remarkably free from suspended matter.

Below station A the river flows westwards and in the remainder of its course becomes polluted by domestic refuse and coal dust from colliery workings. About 10 miles from its source it joins the River Lougher which reaches the sea near Llanelly.

The Nant Garw (nant = brook, garw = rough or stony) rises in very thin, rocky soil at an altitude of about 1500 ft. Its head-streams are of curious type; here and there they form trenches 1–2 ft. wide and 1–2 ft. deep, filled with a jumble of large stones up to ground level. In dry weather no water flow is visible, though it may be heard running below. At 1200 ft. these merge to form a stream of normal type. All collecting was carried out between the points marked *B*. Over this stretch the valley is open and treeless, the stream-bed is 5–15 ft. wide and remarkably uniform in slope, everywhere strewn with innumerable stones rather restricted in size range, the majority being between the size of an egg and a man's head. Large boulders are rare, fine deposits, other than the coarsest gravel, absent. Pools are small, stone-bottomed. The liverwort, *Aplozia*, grows in fair quantity, also a little moss, *Fontinalis antipyretica*. In summer the tops of emergent stones bear dark, withered tufts of bryophytes which grew in winter and spring when the general level of the water was higher. The water is normally clear and quite colourless. At about 500 ft. the stream joins the Amman.

The Nant Pedol has its source in peaty soil at an altitude of 1500 ft. Near its source is a large, marshy, peat-bottomed pond (Llyn-y-fignyn-felin) of acid water (pH 4·4). One of the head-trickles of the Garw rises nearby (Fig. 1, *b*). This is nearly always dry, but after heavy rain carries very yellow water of pH 4·0. At station C the Pedol descends very swiftly; its bed is very largely composed of long slopes of flat rock down which the water pours in thin sheets. Between these rocky slopes are small stony pools, occasionally with deposits of sand and gravel. *Aplozia* grows plentifully, and by the end of the sunny August of 1947 most of the little pools were soupy with green algal growth. The valley is open, a wilderness of heather and ferns. Below 1000 ft. the valley narrows, becoming almost gorge-like and the stream-bed gradually becomes less rocky. At station D the stream-bed is about 20 ft. wide, stony and irregular, with many small pools strewn with dead leaves and other debris. Here the stream is shaded by trees, and in the absence of strong sun the heavy algal growth seen in its upper reaches is no longer evident. About half a mile below station D the stream joins the Amman.

At and above the regions studied all three southern streams are free from any type of pollution; the Garw and Pedol are utilized as sources of water supply.

The Clydach, one of the finest trout streams in the district, rises in springs at an altitude of about 1710 ft. At first the stream flows westwards and its gradient at station E is comparatively gentle. Its bed, for the most part is about 4 ft. wide, and there are many long pools with bottoms of flat rock and gravelly deposits. At one point the gradient is very gentle and the stream, like a miniature river, meanders into shallows where there is a considerable growth of various grasses, mosses and a little *Potamogeton*. Elsewhere macroflora is lacking, and where the water runs swiftly there are few loose stones, the majority being so firmly embedded in the bottom as to be immovable. Nearly all the animals in this region live in the gravel bottom, in grasses immersed at the stream margins, or in the meanders described above. Below station E the stream turns north-west and the valley narrows; at Pont Clydach (station F) the gradient reaches a maximum (660 ft. per mile) and the stream is descending in cascades, pools 10–20 ft. wide alternating

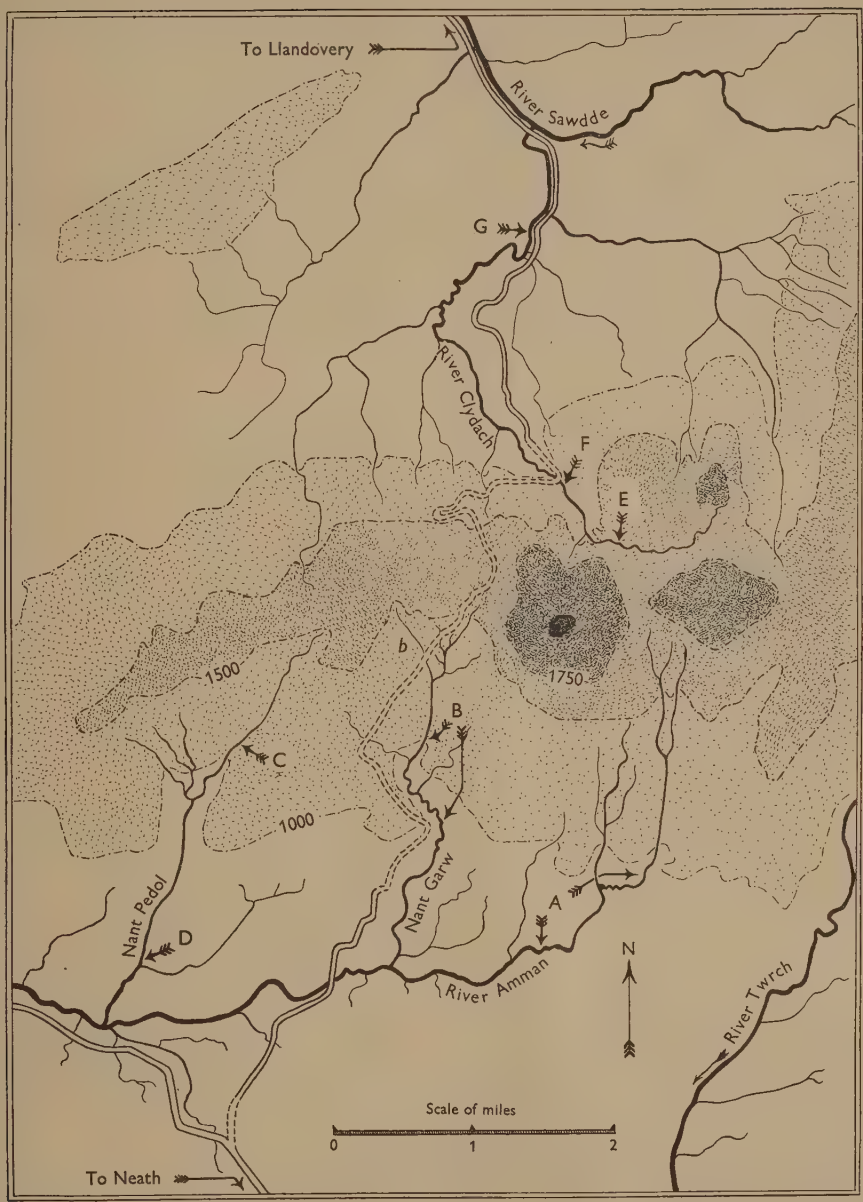


Fig. 1. Map of the district showing the streams studied and the position of the collecting stations. Contours are drawn for 1000, 1500 and 1750 ft. and land over 2000 ft. is shown black.

with little waterfalls. The bed is stony, the stones of all sizes from pebbles to very large boulders. The large pools are clear, between them the water pours over great masses of *Fontinalis antipyretica*. In the shelter of the largest boulders are little pools with sand-gravel bottoms.

At station G (Pont Aber) the stream has greatly changed. Its gradient has slackened to about 50 ft. per mile, it flows through richly wooded and cultivated country and is shaded by trees. Its bed is 20–30 ft. wide, generally covered with stones, pebbles and gravel, occasionally rocky. Its slope is uniform, the water shallow and swift. The instability of the bed appears unfavourable for macroflora, but a little *Fontinalis* grows on some of the larger stones. About a mile below station G the Clydach joins the River Sawdde, one of the main tributaries of the River Towy.

as barium sulphate, and magnesium figures are turbidimetric estimations as magnesium ammonium phosphate. This method for magnesium is reasonably satisfactory if the samples and standards are allowed to stand at least an hour after adding microcosmic salt and ammonia, and frequently stirred. Samples were concentrated by boiling, as necessary, filtered if turbid. Alkali reserve was measured by titrating (to pH 4·4), boiling 250 ml. samples with N/100-hydrochloric acid, using methyl red as indicator. Hydrogen-ion concentrations were determined colorimetrically with bromo-cresol-green, chloro-phenol-red, bromo-thymol-blue and cresol-red (B.D.H. sealed tube standards).

The results show that the Amman, Garw and Pedol all have soft water, the mineral content of the Garw being particularly low. The Clydach has a hard water,

Table 1. *Chemical data*

Alkali reserve is given in normality and pH in the usual units. All other figures are mg. per litre. tr., trace; n.m., not measurable; a dash implies no determination

Station	Date	Level	pH	Alkali reserve	Ca	Mg	Fe'''	Cl	SO_4
Amman A	19 Dec. 1947	Normal	5·2	n.m.	2·8	1·2	tr.	8·8	9·0
	27 Dec. 1947	Full flood	4·4	n.m.	2·2	0·5	0·15	12·4	1·0
Garw B	18 Dec. 1947	Normal	6·4	0·00007	1·8	2·0	n.m.	9·2	3·5
	27 Dec. 1947	Full flood	6·0	0·000024	—	1·0	n.m.	9·2	tr.
Pedol D	22 Dec. 1947	Normal	5·8	0·00002	3·2	2·0	n.m.	12·8	14·0
	27 Dec. 1947	Full flood	4·4	n.m.	2·4	1·5	0·12	14·8	1·5
Clydach F	30 Sept. 1947	Normal	7·4	0·0011	23·0	4·5	n.m.	12·0	—
	28 Dec. 1947	Med. flood	7·0	0·00037	7·6	1·5	n.m.	10·0	tr.
	4 Jan. 1948	Full flood	6·8	0·00020	4·8	—	—	—	—
Clydach G	30 Sept. 1947	Normal	7·8	0·0014	25·8	5·0	n.m.	12·0	—
	28 Dec. 1947	Med. flood	7·2	0·00052	10·8	3·5	n.m.	11·3	tr.
	4 Jan. 1948	Full flood	6·8	0·00028	6·5	—	—	—	—

The Clydach is much less variable in flow than the other three streams studied. It is much less subject to heavy floods and throughout the drought of August 1947 maintained its abundant flow with little obvious diminution while the Amman, Garw and Pedol shrank to mere trickles.

(*c*) *Chemical*

When the fauna samples were taken facilities were not available for making detailed analyses of the stream water, but rough tests showed that the southern slope streams had soft water whereas that of the Clydach is calcareous. The results of further chemical work in September and December 1947 and January 1948 are set out in Table 1. The methods used require little description; calcium was measured by precipitating as oxalate, dissolving in sulphuric acid and titrating with standard permanganate; chloride volumetrically with silver nitrate; iron colorimetrically with hydrochloric acid and ammonium thiocyanate. Sulphate figures are rough turbidimetric estimations

though here again the mineral content is quite moderate in comparison with that of a typical calcareous stream such as the Wembury stream studied by Pantin (1931), which contains over 40 mg. per litre of chloride, 14 mg. per litre of magnesium and over 64 mg. per litre of calcium.

In July it was noticed that the pH of all the streams varied according to conditions, and between 3 July 1947 and 10 January 1948 about sixty determinations on various dates, and with the streams at various levels, showed that the pH fluctuation forms a pattern which is set out in Fig. 2, which shows how the acidity of all four streams increases at flood time. In the case of the Clydach this may be attributed to dilution of its normal spring water by surface water containing less mineral matter, for Table 1 shows that at flood time the calcium content and alkali reserve are greatly reduced. In the case of the Garw, Amman and Pedol the marked rise in acidity at high levels is probably due to the fact that in flood they draw a much greater proportion of their water from

the peaty soils at high altitudes, where acids may have accumulated during dry spells. Thus increased acidity in the Garw is mainly attributable to temporary influx of peaty water, via the streamlet *b* referred to above.

(*d*) *Gradient and current speed*

The profiles of the four streams show that the Clydach is decidedly the most variable in gradient and the Garw, perhaps, the most uniform. At normal or low level the rate of flow of the surface is extremely variable in all the streams, and particularly at station F; here the water may fall almost vertically in places while on the surface of the large pools a float may remain stationary. At flood time the current becomes more uniform at stations A, B, D and G and it is possible to measure the rate of flow of the surface water by timing the movement of floats in mid-stream. A number of trials at various points at stations B and D gave results of about 4 ft. per sec. at medium flood and 5–6 ft. per sec. at full flood. Here it is obvious that the movement of the water is greatly restricted by the stones on the stream bed,

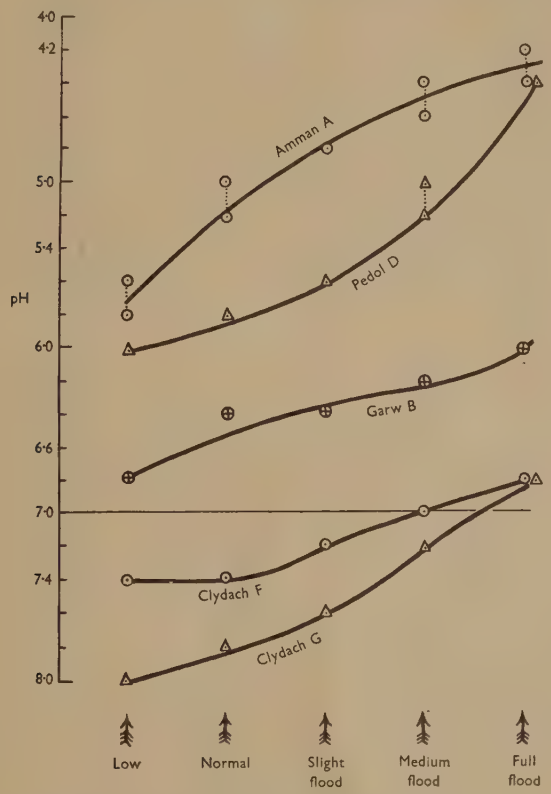


Fig. 2. Summary of hydrogen-ion concentration data for the Amman at station A, the Garw at station B, the Pedol at station D and the Clydach at stations F and G.

Table 2. *Hydrogen-ion concentration data upon which Fig. 2 is based*

The pH determinations were made on various dates between 3 July 1947 and 10 January 1948

Stream level	Amman (A)	Garw (B)	Pedol (D)	Clydach (F)	Clydach (G)
Low	5·6–5·8	6·8	6·0	7·4	8·0
Normal	5·0–5·2	6·4	5·8	7·4	7·8
Slight flood	4·8	6·4	5·6	7·2	7·6
Medium flood	4·4–4·6	6·2	5·0–5·2	7·0	7·2
Full flood	4·2–4·4	6·0	4·4	6·8	6·8

for even at full flood the water only just covers the largest stones. In the Amman at station A there are places where the flood water has a clear channel comparatively free from obstructions, and here, at full flood, floats will move at 7–9 ft. per sec. No consistent result could be obtained at station F, but at station G, with the river in full flood after the heavy rains of the first week of January 1948, floats moved at 4–5 ft. per sec. in mid-stream. It would appear that the rate of flow is determined more by the bulk of water carried and the extent to which it is obstructed by the irregularities of the bed than by the gradient. Thus the River Rheidol, at Aberystwyth, has a surface velocity of just over 5 ft. per sec. in flood though its gradient is only 10 ft. per mile, and considerably greater speeds are attained in very large rivers. Thus, according to data collected by Berg (1943, p. 100), the Volga may flow, at high water, at 7·8–10·1 ft. per sec. and the maximum velocity for the Rhine is about 13 ft. per sec.

(*e*) *Temperature*

During August and September the temperature variation of the water of all four streams was kept under observation. It was not possible to make any detailed study of diurnal swings, but a little preliminary observation showed that on sunny days the stream water generally attained a maximum temperature at between 12.30 and 14.00 hr. (G.M.T.), and subsequently attention was concentrated on the relation between the maximum water temperatures reached and the maximum shade readings on the same day. The pattern of the results is set out in Table 3 and Fig. 3; these readings were all taken on sunny days in August and September between 12.30 and 14.00 hr. For obvious reasons it was not possible to take the shade readings at the collecting stations, and air temperatures were all taken in the shade of buildings about 1½ miles east of station D at an altitude of 600 ft. No readings were taken if the day were dull, or if the sun were obscured by clouds for any considerable period.

The water temperatures were taken with a thermometer of the ordinary type held in the flowing water in mid-stream. In each stream the experiment was tried of thrusting a brass-cased thermometer beneath large stones on the bed. Readings obtained in this way were 0·2–0·5° C. below that of the flowing water nearby, which indicates that animals sheltering beneath the stones are subjected to temperatures very nearly the same as those prevailing in the open water.

Fig. 3 shows that in summer the Clydach has much cooler water than the streams on the southern slopes. This can be attributed, obviously, to its situation on the northern side of the mountain, to its more abundant flow of water and, at station G, to tree shade. It will be noted that over the maximum shade temperature range 17–26° C., a range which must cover most days of a British summer, the maximum water temperature range is only 14·4–18° at station F. On the other hand, the Amman and Garw, with their south aspect and open, treeless valleys are warm streams. All the readings for the Garw are within one degree of the shade temperature, and over the lower portion of the curve for the Amman it will be seen that the water reading is higher than the shade reading, in one instance by 2°. Laurie (1942*a*, p. 370) made a similar observation in the case of the little Afon Tuen near Aberystwyth.

The Pedol at station D is comparatively cool (maximum 19·8°). This is because the stream is shaded by trees for nearly a mile above the point at which the temperatures were taken. Nearer its source, where this shade is lacking, the shade-water temperature relation resembles that of the Garw.

3. THE FAUNA

(*a*) *Collecting methods*

On each occasion about ¾ hr. was spent in collecting at each station. As in previous studies by the writer, no quantitative sampling was attempted and attention was concentrated on capturing as many species as possible and noting their degree of abundance. At points where the water runs swiftly, stones on the stream-bed were overturned and brushed with the hand so that animals clinging upon and beneath them were swept by the current into a large D-section water net held immediately downstream. Any bryophyte growth on the upper side of the stone was thoroughly combed with the fingers and shaken in front of the net before the stone was moved. Stones on the bottom of pools were roughly overturned while the net was swept to and fro in the surrounding water. Special attention was paid to grass on submerged clods, as this was found to harbour many beetles. All material accumulating in the net was transferred to water in a large collecting jar.

The use of sieves was found unnecessary as no mud deposits occur, and animals sheltering in sand and gravel could be captured very successfully by violently stirring up the deposit with the foot, allowing it one or two seconds to settle, and then sweeping the net through the water above. Stones were also removed from the water and examined for the capture of animals not readily dislodged; this procedure is also necessary to show whether the distribution of the animals is patchy or uniform.

The collecting jar was emptied into white dishes at the laboratory, the larger animals being picked out first and counted. The debris which settled on the bottom of the dishes was pipetted into Petri dishes and examined with a low-power, wide-field binocular.

Table 3. *Temperature records upon which Fig. 3 is based*

Date (1947)	Maximum shade temperature (° C.)	Maximum water temperatures (° C.) Amman A	Garw B	Pedol C	Pedol D	Clydach F	Clydach G
11 Aug.	24·0	—	23·0	—	—	—	—
12 Aug.	25·0	—	—	—	—	16·5	17·0
13 Aug.	26·0	—	—	—	19·8	18·0	—
14 Aug.	25·0	23·5	24·5	—	19·3	—	—
15 Aug.	25·5	—	25·2	—	—	—	—
20 Aug.	25·2	—	24·6	24·4	—	—	—
21 Aug.	25·0	—	—	—	—	17·4	17·7
22 Aug.	23·0	21·5	—	—	—	15·3	—
25 Aug.	22·0	—	—	21·8	17·7	—	—
3 Sept.	21·0	19·7	20·4	—	—	—	—
4 Sept.	19·0	—	—	—	15·5	14·9	—
5 Sept.	18·0	18·4	—	—	—	—	—
7 Sept.	17·1	18·2	—	16·2	—	—	—
10 Sept.	17·0	—	—	—	—	14·4	15·3
11 Sept.	20·0	—	—	—	16·3	—	—
13 Sept.	16·0	17·7	16·5	—	—	—	—
21 Sept.	15·0	17·0	—	—	14·7	13·0	14·0
22 Sept.	12·0	—	—	—	—	9·6	10·4

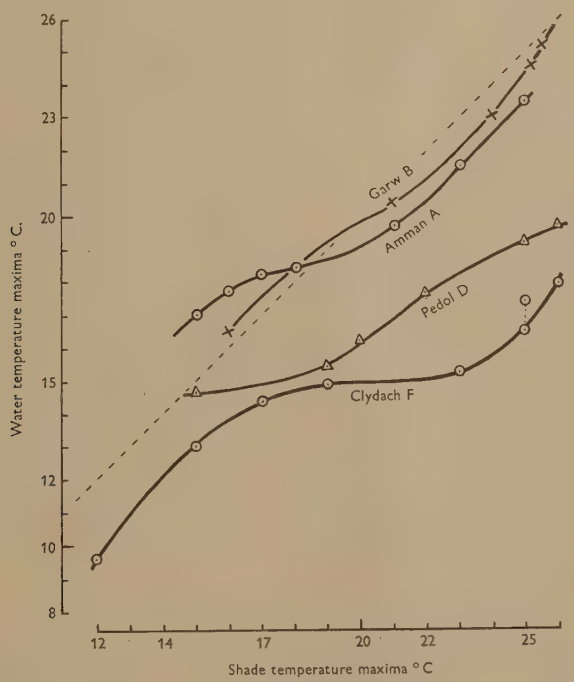


Fig. 3. The maximum shade temperature/maximum water temperature relation for the Amman at station A, the Garw at station B, the Pedol at station D and the Clydach at station F. All readings were taken on sunny days as explained in the text. At station G the temperature of the Clydach was always 0·3–1·0° C. above that at station F on the same day.

(*b*) *The species recorded*

All the animals are listed in Table 4. Wherever possible the actual number of individuals captured at the collecting station is given; when this number is between 100 and 200 the symbol N (numerous) is inserted, and VN (very numerous) signifies that the number captured could be estimated at many hundreds.

The works consulted for identification include those listed by Laurie (1942*b*) and in addition the following: Kimmins (1942) for Ephemeroptera (nymphs and subimagines and imagines bred out), Hynes (1940) for Plecoptera bred out, Kimmins (1943) for Neuroptera; Simuliidae with the aid of Puri (1925) and Smart (1944). For Diptera, Johannsen (1934, 1935, 1937), and Goetghebuer (1927, 1928, 1932). Trichopteran pupae in which the genetalia showed clearly could be specifically identified with the aid of Mosely's monograph on the adults (1939), and some Trichopteran larvae could be identified with reasonable certainty by comparison with specimens of larvae bred out at Aberystwyth. Sars (1928) was used for the identification of Ostracoda and Dr E. E. Watkin has kindly checked the identification of *Gammarus pulex*.

Brown trout are plentiful in the Clydach, which is a preserved fishing, and salmon spawn there. Trout also occur in the Garw and Pedol, but have little chance to thrive, for the fishing is neither fostered nor protected. Minnows occur in the Garw in small numbers but in the Amman no fish seem to occur above its confluence with the Garw.

(*c*) *Remarks on the fauna*

Taken as a whole the fauna is rich, for the number of species represented (about 151) exceeds the number recorded by Carpenter (1927) for the whole of north Cardiganshire including the plateau streams, lowland streams and longer rivers. Of the four streams the Clydach, with about 130 species, has by far the richest and most varied fauna. Many factors probably contribute to this—its wider range of habitat, its varying gradient, more abundant macroflora, alkaline-neutral water and its more abundant and more uniform flow. It is also possible that its more equable temperature may be a further favourable factor. As the dominant animals of the stream we may pick out *Polycelis cornuta*, *Gammarus*, *Perla*, the Ephemeroptera (particularly the lithophilous types), *Velia*, campodeiform Trichoptera and the trout. *Polycelis cornuta* occurs gregariously under stones at station E and in little tributaries nearby, and it is interesting to note that in this district it has been found only above 1500 ft., whereas in north Cardiganshire Carpenter (1928, p. 112) and the writer (1940) found this 'glacial relict' of the Alps and Harz mountains confined to lowland streams. *Gammarus* at station E lives in the bottom gravel and at F in the moss of little marginal pools. Atkins (1923, p. 205) says that *G. pulex* soon dies if placed in water less alkaline than pH 7·4. In the Clydach it is evidently able to survive at least temporary subjection to a pH of 6·8–7·2. *Gammarus* is definitely less abundant at station F than at E, and at G has practically disappeared although the stream is generally more alkaline at this point.

The distribution of *Dinocras cephalotes* and *Perla carlukiana* agrees with the observations of Hynes (1940, p. 33), who finds that in the Lake District *cephalotes* likes a stream with a stable, mossy bottom, and *carlukiana* a river with a loose, unstable bottom. At least two species of *Baetis* are abundant everywhere; these were not bred out, but the dominant one appears to be *rhodani*, the commonest species in the Aberystwyth district. The only species of *Sigara* at all common is *nigrolineata*. Macan (1938) states that this is one of the dominant species of Corixidae in Lake District pools above 1300 ft.

In spite of the alkalinity and moderate calcium content of the water, Mollusca are not common. This may be attributed to the rapid flow of the stream. Boycott (1936, p. 166) observes that 'Water which runs too fast is relatively sterile....No Mollusca except the larger bivalves, adult *Dreissena* and *Ancylus* can avoid being swept away by the current and in floods even these will be killed by the moving stones. Hence violent streams generally contain no molluscs' The few *Limnaea pereger* recorded from station G were found under stones at the margins.

One animal group, the Hirudinea, is conspicuously unrepresented in the Clydach. However, there is little evidence that leeches are common in unpolluted streams of this type. In the River Dovey at 500 ft. and above, the writer (1941, p. 18) found only two specimens of *Herpobdella*. In a recent survey of the ecology of leeches in Denmark Bennike (1943, p. 102) notes that *Herpobdella octoculata*, *Glossosiphonia complanata* and *Helobdella stagnalis* are the only species common in brooks, though a rich leech fauna may be found in rivers with a broad vegetation zone. The absence of *Glossosiphonia* may be due to the lack of suitable food, for this leech feeds mainly upon Mollusca; the absence of *Herpobdella* and *Helobdella* must be due to some other factor for the diet of these species, according to Bennike (1943, pp. 73, 91), consists largely of chironomid larvae.

Of the three southern streams the Garw, with about 65 species, has the richest fauna. Only 9 species other than insects occur, and of these only *Hygrobates naicus* is at all common and well distributed. The dominant animals are all insects—*Baetis*, *Velia*, *Philopotamus*, *Simulium*, and the little Trichopteran larvae *Hydroptila* and *Oxyethira* which appear to flourish

Table 4. *The fauna*

The figures give the number of specimens captured at the collecting stations; thus each is a sum-total for six fauna samples at station A, seven at B, etc. N and VN stand for 'numerous' and 'very numerous' as explained in the text. Nomenclature of the insects follows Kloet & Hincks (1945), except in the cases of *Nemoura* and *Sigara*, which are retained as generic names in more general use.

	Amman	Garw	Pedol		Clydach		
Collecting station	A	B	C	D	E	F	G
Collecting dates (year 1947)	16 July 2 Aug. 22 Aug. 3 Sept. 8 Sept. 12 Sept.	5 July 9 July 16 July 23 July 27 July 20 Aug. 9 Sept.	10 July 29 July 25 Aug. 26 Sept.	19 July 28 July 12 Aug. 11 Sept.	15 July 5 Aug. 18 Aug. 30 Aug. 23 Sept. 27 Sept.	15 July 19 July 1 Aug. 13 Aug. 26 Aug. 5 Sept.	14 July 18 July 29 July 8 Aug. 21 Aug. 10 Sept.
HYDROZOA							
Hydra viridissima Pall.	—	—	—	—	1	—	—
H. vulgaris Pall.	—	—	—	—	—	1	3
PLATYHELMIA							
Polycelis cornuta (Johnson)	—	—	—	—	N	—	—
Planaria vitta Dugès	2	—	1	—	—	—	1
P. alpina (Dana)	—	2	—	—	26	2	16
OLIGOCHAETA							
Eiseniella sp.	—	—	—	—	2	2	—
Lumbriculus variegatus (Müll.)	—	8	—	—	1	—	—
Nais sp.	—	—	—	—	—	7	4
Other spp.	—	—	—	—	—	—	3
GORDIACEAE							
Gordius sp.	—	—	—	—	2	—	—
MOLLUSCA							
Limnaea pereger (Müll.)	—	—	—	—	—	—	28
L. truncatula (Müll.)	—	25	—	—	—	—	—
Ancylastrum fluviatile (Müll.)	—	—	—	—	—	—	8
CRUSTACEA							
Gammarus pulex (L.)	—	—	—	—	VN	N	10
Cyclops agilis Koch, Sars	—	—	—	—	46	—	—
Cypridopsella villosa (Jurine)	—	—	—	—	3	—	—
Herpetocypris reptans (Baird)	—	—	—	—	26	8	3
HYDRACARINA							
Protzia exemia (Protz)	—	—	—	—	3	—	—
Sperchon longirostris Koen.	—	—	—	1	—	22	—
S. brevirostris Koen.	—	—	—	—	—	—	33
S. papillosus Sig Thor	—	—	—	—	—	—	2
S. tenuabilis Koen.	—	—	—	—	—	1	—
S. denticulatus Koen.	4	—	—	—	—	—	2
S. clupeifer Piers.	—	—	—	—	—	—	8
Pseudosperchon verrucosus (Protz)	—	—	—	—	—	—	1
Lebertia celtica Sig Thor	2	3	—	—	—	—	15
Lebertia sp. *a*	1	2	—	—	—	—	—
Atractides amplexus Koen.	—	—	—	—	—	2	—
A. brevirostris Halb.	—	2	—	—	—	1	14
Hygrobates naicus (Jonst.)	15	42	3	32	4	10	9
Megapus spinipes (C.L. Koch)	—	—	1	3	—	3	17
Ljania bipapillata Sig Thor	—	—	—	—	—	—	1
Aturus scaber Kram.	—	—	—	—	—	—	2
Kongsbergia materna Sig Thor	—	—	—	—	—	—	1
COLLEMBOLA							
Isotomurus palustris (Müll.)	—	—	7	—	3	—	—

Table 4 (*cont.*)

	Amman	Garw	Pedol		Clydach		
Collecting stations	A	B	C	D	E	F	G
Collecting dates (year 1947)	16 July 2 Aug. 22 Aug. 3 Sept. 8 Sept. 12 Sept.	5 July 9 July 16 July 23 July 27 July 20 Aug. 9 Sept.	10 July 29 July 25 Aug. 26 Sept.	19 July 28 July 12 Aug. 11 Sept.	15 July 5 Aug. 18 Aug. 30 Aug. 23 Sept. 27 Sept.	15 July 19 July 1 Aug. 13 Aug. 26 Aug. 5 Sept.	14 July 18 July 29 July 8 Aug. 21 Aug. 10 Sept.
PLECOPTERA							
Perlodes sp.	—	12	—	2	11	12	—
Dinocras cephalotes (Curt.)	—	—	—	—	—	59	20
Perla carlukiana Klap.	—	—	—	—	—	—	N
Isoperla grammatica (Poda)	—	7	—	—	—	1	—
Chloroperla torrentium (Pict.) (bred out)	9	19	—	82	6	1	3
Leuctra geniculata Steph. (bred out)	—	—	—	—	—	—	14
L. fusciventris Steph. (bred out)	8	68	14	52	19	52	N
[1]Nemoura praecox (Mort.) (bred out)	—	—	—	65	1	6	8
N. inconspicua (Pict.)	—	—	—	—	6	6	—
N. (Amphinemura) sp. *a*	1	12	—	1	1	4	30
EPHEMEROPTERA							
[2]Baëtis spp.	—	VN	5	N	VN	VN	VN
Ephemerella notata Eaton (bred out)	—	42	—	—	5	N	N
Paraleptophlebia sp.	—	—	1	—	1	2	4
Caenis sp.	—	—	—	—	—	—	4
Rhithrogena sp.	—	—	—	—	—	2	2
Heptagenia sp.	—	35	—	—	3	10	—
Ecdyonurus venosus (Fab.) (bred out)	—	—	—	—	1	N	N
Siphlonurus lacustris Eaton (bred out)	—	—	—	—	N	7	—
HEMIPTERA							
Hydrometra stagnorum (L.)	—	1	—	1	—	—	—
Velia currens (Fab.)	VN	VN	N	24	VN	VN	9
Gerris thoracicus Schum.	—	—	—	—	1	—	—
G. gibbifera Schum.	25	6	6	1	59	2	—
G. lacustris (L.)	—	—	—	—	2	1	—
Gerris spp. nymphs	17	—	2	—	7	12	2
Notonecta viridis viridis Delc.	—	—	—	—	1	—	—
N. maculata Fab.	4	—	—	—	—	—	—
N. obliqua obliqua Gall.	3	—	—	—	—	—	—
Sigara castanea (Thoms.)	1	—	—	—	1	—	—
S. sahlbergi (Fieb.)	—	—	—	—	2	—	—
S. striata (L.)	—	—	2	—	1	—	—
S. nigrolineata Fieb.	5	—	—	—	26	—	—
Sigara spp. nymphs	—	4	—	—	—	—	2
ODONATA							
Ischnura elegans (van der Lind.)	2	1	—	—	—	7	—
Cordulegaster boltonii (Don.)	2	—	—	1	2	3	—
MEGALOPTERA							
Sialis fuliginosa Pict.	4	—	8	—	—	—	—
TRICHOPTERA							
Stenophylax stellatus (Curt.)	—	—	28	—	—	—	12
Halesus sp.	—	1	—	1	4	10	2
Sericostoma personatum (Spence)	—	—	—	—	—	2	14
Goëra pilosa (Fab.) (pupae)	—	—	—	—	—	—	2
Odontocerum albicorne (Scop.)	—	2	—	—	—	7	6
Hydropsyche instabilis (Curt.)	—	3	—	—	—	—	N

[1] This identification is based on one specimen from station E which bred out to *praecox*; it is possible that the more common *meyeri* (Pict.) also occurs.

[2] *Baetis rhodani* (Pict.) and at least one other species.

Table 4 (*cont.*)

	Amman	Garw	Pedol		Clydach		
Collecting station	A	B	C	D	E	F	G
Collecting dates (year 1947)	16 July 2 Aug. 22 Aug. 3 Sept. 8 Sept. 12 Sept.	5 July 9 July 16 July 23 July 27 July 20 Aug. 9 Sept.	10 July 29 July 25 Aug. 26 Sept.	19 July 28 July 12 Aug. 11 Sept.	15 July 5 Aug. 18 Aug. 30 Aug. 23 Sept. 27 Sept.	15 July 19 July 1 Aug. 13 Aug. 26 Aug. 5 Sept.	14 July 18 July 29 July 8 Aug. 21 Aug. 10 Sept.
TRICHOPTERA (*cont.*)							
H. pellucidula (Curt.)	—	8	—	—	—	—	11
Plectrocnemia conspersa (Curt.)	17	28	15	25	39	6	5
P. conspersa (pupae)	—	—	—	—	5	—	—
Polycentropus flavomaculatus (Pict.)	N	9	1	11	—	—	—
Philopotamus montanus (Don.)	—	N	—	—	2	7	22
Wormaldia subnigra McLachl. (pupa)	—	—	—	—	—	—	1
[1]Rhyacophila sp. *a*	42	26	6	53	17	15	68
[2]Rhyacophila sp. *b*	—	2	—	—	—	11	—
R. dorsalis (Curt.) (pupae)	—	—	—	6	—	—	—
Glossosoma boltoni Curt.	—	—	—	—	—	—	4
Agapetus fuscipes Curt.	—	—	—	—	N	—	—
Hydroptila sp.	—	VN	—	—	—	2	—
Oxyethira sp.	14	45	1	—	—	2	—
COLEOPTERA (imagines)							
Haliplus lineatocollis (Marsh.)	2	2	—	—	1	1	—
Deronectes latus (Steph.)	19	2	—	1	1	1	1
D. duodecimpustulatus (Fab.)	4	—	12	—	1	—	—
D. elegans (Panz.)	—	—	2	—	2	2	1
Oreodytes davisii (Curt.)	19	—	—	—	2	—	—
O. septentrionalis (Gyll.)	9	1	4	—	—	9	3
O. rivalis (Gyll.)	9	14	9	4	—	46	5
Hydroporus lepidus (Oliv.)	6	1	18	—	—	—	—
H. tristis (Payk.)	4	—	—	—	8	—	—
H. palustris (L.)	1	—	—	—	—	—	—
H. nigrita (Fab.)	7	—	3	—	4	3	3
H. pubescens (Gyll.)	1	—	—	—	—	—	—
Rantus pulverosus (Steph.)	—	—	1	—	—	—	—
R. bistriatus (Bergstr.)	—	—	2	—	—	—	—
Ilybius fuliginosus (Fab.)	1	—	—	—	—	—	—
Agabus bipustulatus (L.)	14	1	—	—	2	—	—
A. didymus (Oliv.)	1	—	—	—	—	—	—
A. guttatus (Payk.)	—	4	6	—	3	4	—
Acilius sulcatus (L.)	2	—	—	—	—	—	—
Dytiscus marginalis L.	1	—	—	—	3	—	—
Limnebius truncatellus (Thunb.)	—	3	3	—	7	3	1
Laccobius alutaceus Thoms.	—	1	—	—	2	6	—
L. minutus (L.)	2	—	4	—	—	3	—
Anacaena globulus (Payk.)	3	4	4	—	2	8	—
Helophorus flavipes Fab.	—	3	—	—	2	5	—
H. brevipalpis Bed.	5	—	—	1	1	3	—
Hydraena pygmaea Waterh.	—	—	—	1	—	—	—
H. gracilis Germ.	1	6	1	2	4	3	51
Latelmis volkmari (Pz.)	8	5	2	2	13	8	8
Elmis maugei Bed.	7	21	5	10	11	12	8
Esolus parallelopipedus (Müll.)	3	2	5	—	2	13	—
Limnius tuberculatus (Müll.)	—	20	—	—	2	1	—
Gyrinus spp.	21	26	—	—	45	—	—
Dryops luridus Erichs.	—	4	—	—	10	2	—

[1] With gills in bunches of 10–20 as *Rhyacophila dorsalis* (Curt.) and *R. obliterata* McLachl.
[2] With gills in bunches of four as in the continental species *R. glareosa* McLachl.

Table 4 (*cont.*)

	Amman	Garw	Pedol		Clydach		
Collecting station	A	B	C	D	E	F	G
Collecting dates (year 1947)	16 July 2 Aug. 22 Aug. 3 Sept. 8 Sept. 12 Sept.	5 July 9 July 16 July 23 July 27 July 20 Aug. 9 Sept.	10 July 29 July 25 Aug. 26 Sept.	19 July 28 July 12 Aug. 11 Sept.	15 July 5 Aug. 18 Aug. 30 Aug. 23 Sept. 27 Sept.	15 July 19 July 1 Aug. 13 Aug. 26 Aug. 5 Sept.	14 July 18 July 29 July 8 Aug. 21 Aug. 10 Sept.
COLEOPTERA (larvae)							
Agabus guttatus (Payk.)	—	—	66	—	—	—	—
Dytiscidae other spp.	—	16	3	—	6	6	4
Helodidae	—	5	—	—	5	10	—
[1]Elminae	—	1	1	—	32	N	63
Other Dryopidae	—	—	—	—	3	1	2
DIPTERA							
Tipula sp.	—	2	2	1	—	—	—
Dicranota sp.	6	6	5	10	24	82	39
Pedicia sp.	—	—	—	—	1	2	—
Dicranomyia sp.	—	—	—	—	—	1	—
Phalacrocera sp.	—	—	—	—	—	1	—
Limnophila sp.	1	2	—	—	—	3	1
Prionocera sp.	—	—	1	—	—	—	—
Pericoma sp.	—	1	—	—	—	—	1
Dixa sp.	—	—	—	1	—	4	5
[2]Ceratopogonidae	—	1	—	2	—	2	—
Macropelopia sp.	41	1	2	3	3	95	1
Pentaneura sp.	21	2	15	—	20	22	6
Prodiamesa olivacea (Mg.)	—	—	—	1	33	11	—
Corynoneura sp.	—	—	—	1	N	11	—
Cricotopus sp.	—	—	—	—	—	2	—
Spaniotoma sp.	35	—	—	—	—	—	3
[3]Tanytarsus (sensu lato) sp.	2	—	—	—	—	2	—
[4]Other Chironomidae	N	9	N	N	24	70	73
Simulium latipes (Mg.)	13	17	—	44	5	9	1
S. aureum Fries.	—	2	—	—	—	—	3
S. angustitarse Lundstr.	—	8	—	—	—	—	—
S. variegatum Mg.	—	N	—	2	16	—	—
S. ornatum Mg.	2	1	—	—	—	3	—
S. tuberosum Lundstr.	—	4	—	—	—	—	27
PISCES							
Salmo trutta L. (brown trout) S. salar L. (salmon) Phoxinus phoxinus (L.) (minnow)	See text						
AMPHIBIA							
Rana temporaria L. (frogs)	—	—	—	—	3	—	—
Bufo bufo (L.) (tadpoles)	—	—	—	—	21	—	—

[1] Mainly of *Elmis maugei*.
[2] Larvae of *Bezzia* type.
[3] My larvae agree well with the description of *Lauterbornia gracilenta* (Holingr.) given by Goetghebuer (1928), but the species has not been recorded from Britain.
[4] Immature larvae mainly.

in the masses of algal growth on the stream-bed. Many factors probably combine to limit the fauna: the uniform nature of the stream-bed, the lack of macroflora, the acidity and softness of the water, and frequent violent floods. The disastrous effects of flooding on benthoplankton have been reviewed by Denham (1938), and there is little doubt but that this factor must be a very important one in the present case, for a single day of heavy rain is sufficient to convert the stream into a roaring torrent. The uniform slope of the stream-bed probably increases the effect of floods; it is possible that in a torrential stream of the cascade type refuge from swiftly flowing water may be found at the bottom of the pools.

As has been pointed out in §2(*e*) the summer temperature of the water is high; but the importance of the temperature factor is not easy to assess, for in spite of much experimental work our knowledge of how far aquatic animals can withstand high temperatures is far from complete. The water temperature attains, or at least approaches, the thermal death point of many aquatic species. Thus Murray (1938), discussing the temperature factor in regard to the distribution of trout and stream-stocking policy, states that brown trout are distressed at 83° F. (29° C.). Heilbrunn (1937, p. 331) states that *Hydra* is killed in Douglas Lake, Michigan, when the daily maximum temperature exceeds 22·2° C. Steinmann (1907) found that *Planaria alpina* dies at 21° C. even if the temperature of the water is raised gradually. Carpenter (1928) considers that in the Aberystwyth area this species has become acclimatized to higher temperatures and found that it would survive for a short period at 22° C. Whitney (1939) found temperatures of 20–24° C. fatal to *Baetis* on sudden transference from 10 to 11° C., and temperatures of 26–28° C. fatal to *Ecdyonurus*. *Baetis* is abundant in the Garw and *Ecdyonurus* absent, which is not in agreement with Whitney's results. Griffiths (1945), working under my direction, found that if the temperature was raised gradually *Ecdyonurus* survived to 37° C. before passing into heat coma. It is possible that the temperature factor does limit the ephemeropteran population of the Garw, but their still poorer representation in the Pedol and complete absence from the Amman rather suggests that high acidity is the main factor involved. Jewell (1922) found an absence of ephemerid nymphs one of the principal features of the Big Muddy River, a tributary of the Mississippi, the acidity of which may rise to pH 5·5. *Hydra* does not occur in the Garw and the temperature factor may well be responsible, and only two specimens of *Planaria alpina* were found. This was on 9 July.

On the other hand, many invertebrates can withstand comparatively high temperatures and it appears to be generally considered that the highest water temperature compatible with animal life is about 50° C. Aquatic beetles in particular appear resistant. Thus Griffiths (1945) found that *Hydroporus palustris* (L.), *Hygrotus inaequalis* (Fab.) and *Deronectes elegans* (Pz.) remained active up to 36°, 37° and 42° C., while *Gyrinus* sp. (which does not normally live immersed) ceased to be active at about 31° C. Pruthi (1939) found *Helochares* and *Coelostoma* in a hot spring at 45° C. Ide (1935), in his study of the effect of temperature on the distribution of Ephemeroptera, concluded that the lower and warmer reaches of streams have a richer ephemerid fauna than the upper reaches, where low temperatures may render it impossible for certain species to grow sufficiently quickly to complete their development. Maximum summer temperatures at Ide's collecting stations ranged from 11 to 30° C.

The Pedol, with about 57 species, has a poorer fauna still. Of the 57 species 19 are beetles and 12 are Diptera. A wider range of habitat is afforded than in the Garw, and in the lower portion of the stream the temperature is more equable, but this little stream is also subject to violent floods and the high and violently swinging acidity of the water is undoubtedly a further adverse factor. The upper part of the stream has a very restricted fauna, the only Plecoptera found here were a few *Leuctra*, the only Ephemeroptera 5 *Baetis* and 1 *Paraleptophlebia*.

Of all four streams the Amman appears the most inhospitable. Like the Garw and Pedol it is subject to frequent floods, runs nearly dry in dry sunny weather; the macroflora is extremely scanty, and generally its water is even more acid than that of the Pedol. Its fauna is limited to insects, and whole insect groups are absent or very poorly represented. Yet the number of species recorded (about 55) is not particularly low. Hemiptera are well represented, and in relation to the absence of vegetation the occurrence of *Notonecta maculata* is interesting, a species in which the ovipositor is adapted for sticking the eggs to a hard substratum. Campodeiform Trichoptera are well represented too; the stomach contents of a few *Plectrocnemia* and *Polycentropus* larvae were examined and these seemed to have been feeding mainly on Chironomid larvae.

Of the 55 species 24 are beetles and it is surprising to find such a variety, for in the whole 80-mile main stream of the River Teifi, with its enormously greater range of habitat, the writer (1943) found only 16 species.

In review the survey would seem to indicate that the fauna of torrential streams does not necessarily conform to a generalized type, and that various factors, gradient, flora, amplitude and constancy of flow, temperature and hydrogen-ion concentration may give individual streams faunas of markedly individual character.

4. SUMMARY

1. This paper is a general study of four torrential streams in the 'Black Mountain' district of south Wales. Fauna collections were made at seven collecting stations, between altitudes of 1550 and 400 ft. Observations were made on the chemical nature of the water, current speed and temperature. The fauna taken as a whole is rich, including about 151 species.

2. Of the four streams, the one flowing north has the richest fauna, which includes about 130 species in which all the usual aquatic animal groups except the Hirudinea are represented. This may be attributed to its equable temperature, abundant and uniform flow, variable gradient, adequate macroflora, and alkaline-neutral moderately calcareous water.

3. The streams flowing south all have very soft, acid water; their stream-beds are more uniform in gradient, they are extremely variable in flow, have a more scanty macroflora, and on sunny summer days the water temperature is high, little below the shade temperature. All have a much poorer fauna than the north-flowing stream. One has a pH of 6·0–6·8, the fauna includes about 65 species, the usual insect groups are well represented but only 9 species other than insects occur. The second has a pH of 6·0 at low level to 4·4 in full flood; here 57 species were found, again mainly insects, and the Ephemeroptera are very poorly represented. The third southern stream is generally even more acid, pH 5·8–4·2. Its fauna includes 55 species of which 24 are beetles, Plecoptera are very poorly represented and Ephemeroptera absent.

REFERENCES

Atkins, W. R. G. (1923). 'The hydrogen ion concentration of the soil and natural waters in relation to diseases other than bacterial.' Parasitology, 15: 205–10.

Bennike, S. A. Boisen (1943). 'Contributions to the ecology and biology of the Danish fresh-water leeches (Hirudinea).' Folia Limnol. Scand. No. 2: 1–109.

Berg, K. (1943). 'Physiographical studies on the river Susaa.' Folia Limnol. Scand. No. 1: 1–174.

Boycott, A. E. (1936). 'The habitats of fresh-water Mollusca in Britain.' J. Anim. Ecol. 5: 116–86.

Carpenter, K. E. (1924). 'A study of the fauna of rivers polluted by lead mining in the Aberystwyth district of Cardiganshire.' Ann. Appl. Biol. 11: 1–23.

Carpenter, K. E. (1927). 'Faunistic ecology of some Cardiganshire streams.' J. Ecol. 15: 33–54.

Carpenter, K. E. (1928). 'On the distribution of fresh-water Turbellaria in the Aberystwyth district, with especial reference to two Ice-Age relicts.' J. Ecol. 16: 105–22.

Denham, S. C. (1938). 'A limnological investigation of the west fork and common branch of White River.' Invest. Indiana Lakes and Streams, No. 5: 17–71.

Goetghebuer, M. (1927). 'Diptères (Nématocères) Chironomidae Tanypodinae.' Faune de France, 15. Paris.

Goetghebuer, M. (1928). 'Diptères (Nématocères) Chironomidae. III. Chironomariae.' Faune de France, 18. Paris.

Goetghebuer, M. (1932). 'Diptères Chironomidae IV. (Orthocladiinae, Corynoneurinae, Clunioninae, Diamesinae).' Faune de France, 23. Paris.

Griffiths, M. E. (1945). 'Some observations on the heat death point of aquatic insects.' Thesis, Library, University College of Wales, Aberystwyth.

Heilbrunn, L. V. (1937). 'An outline of general physiology.' Philadelphia etc.

Hynes, H. B. N. (1940). 'A key to the British species of Plecoptera (stoneflies) with notes on their ecology.' Sci. Publ. Freshw. Biol. Ass. Brit. Empire, 2: 1–39.

Ide, F. P. (1935). 'The effect of temperature on the distribution of the mayfly fauna of a stream.' Univ. Toronto Stud., Biol. Ser. No. 39: 3–76.

Jewell, M. E. (1922). 'The fauna of an acid stream.' Ecology, 3: 22–8.

Johannsen, O. A. (1934). 'Aquatic Diptera Part I. Nemocera, exclusive of Chironomidae and Ceratopogonidae.' Mem. Cornell Agric. Exp. Sta. 164: 1–71.

Johannsen, O. A. (1935). 'Aquatic Diptera Part II. Orthorrhapha—Brachycera and Cyclorrhapha.' Mem. Cornell Agric. Exp. Sta. 177: 1–62.

Johannsen, O. A. (1937). 'Aquatic Diptera Part III. Chironomidae: subfamilies Tanypodinae, Diamesinae and Orthocladiinae.' Mem. Cornell Agric. Exp. Sta. 205: 1–84.

Jones, J. R. E. (1940). 'The fauna of the river Melindwr, a lead-polluted tributary of the river Rheidol in North Cardiganshire, Wales.' J. Anim. Ecol. 9: 188–201.

Jones, J. R. E. (1941). 'The fauna of the river Dovey, West Wales.' J. Anim. Ecol. 10: 12–24.

Jones, J. R. E. (1943). 'The fauna of the river Teifi, West Wales.' J. Anim. Ecol. 12: 115–23.

Kimmins, D. E. (1942). 'Keys to the British species of Ephemeroptera with keys to the genera of the nymphs.' Sci. Publ. Freshw. Biol. Ass. Brit. Empire, No. 7: 1–64.

Kimmins, D. E. (1943). 'Keys to the British species of aquatic Megaloptera and Neuroptera.' Sci. Publ. Freshw. Biol. Ass. Brit. Empire, 8: 1–20.

Kloet, G. S. & Hincks, W. D. (1945). 'A check list of British insects.' Stockport.

Laurie, E. M. O. (1942*a*). 'The dissolved oxygen of an upland pond and its inflowing stream, at Ystumtuen, North Cardiganshire, Wales.' J. Ecol. 30: 357–82.

Laurie, E. M. O. (1942*b*). 'The fauna of an upland pond and its inflowing stream at Ystumtuen, North Cardiganshire, Wales.' J. Anim. Ecol. 11: 165–81.

Macan, T. T. (1938). 'Evolution of aquatic habitats with special reference to the distribution of Corixidae.' J. Anim. Ecol. 7: 1–19.

Mosely, M. E. (1939). 'The British caddis flies (Trichoptera): a collector's handbook.' London.

Murray, M. J. (1938). 'Survey of some Northern Indiana streams with special reference to trout production.' Invest. Indiana Lakes and Streams, No. 7: 79–99.

Pantin, C. F. A. (1931). 'The adaptation of *Gunda ulvae* to salinity. I. The environment.' J. Exp. Biol. 8: 63–72.

Pruthi, H. S. (1939). 'Record of some insects from a hot spring in the Kulu Valley, Punjab.' Indian J. Ent. 1: 65–7.

Puri, I. M. (1925). 'On the life-history and structure of the early stages of Simuliidae (Diptera, Nematocera). Part I.' Parasitology, 17: 295–334, [Part 2] 335–69.

Sars, G. O. (1928). 'An account of the Crustacea of Norway.' Vol. 9 'Ostracoda'. Bergen.

Smart, J. (1944). 'The British Simuliidae with keys to the species in the adult, pupal and larval stages.' Sci. Publ. Freshw. Biol. Ass. Brit. Empire, 9: 1–57.

Steinmann, P. (1907). 'Die Tierwelt der Gebirgsbäche eine faunistisch-biologische Studie.' Ann. Biol. Lac. 2: 30–150.

Whitney, R. J. (1939). 'The thermal resistance of mayfly nymphs from ponds and streams.' J. Exp. Biol. 16: 374–85.

A SHETLAND BIRD POPULATION: KERGORD PLANTATIONS

By L. S. V. VENABLES and U. M. VENABLES

(With Plate 1 and 1 Figure in the Text)

1. INTRODUCTION

Although the more 'popular' descriptive books refer to the 'Treeless Shetlands' (MacDiarmid, 1939, for example) this is far from being the case. They are neither treeless nor, incidentally, are they 'The Shetlands'. Right throughout Shetland innumerable gardens have small clumps of trees and bushes, and though their growth is usually somewhat stunted there are many places where quite sizeable trees are to be found. To cite only a few of these we may mention Lerwick and vicinity, Scalloway, Tresta, Busta, Voxter, Stromfirth and even, well towards the north of Unst at Halligarth, Baltasound. These small clumps of cover are now a marked feature of the Shetland landscape, but Dr Saxby (1874), even in his day, drew attention to the fact that the growth of trees at Halligarth, one of the earliest of the present plantings, was attracting the smaller passerines. In fact he attributed the arrival of several new species solely to these trees.

The presence of roots and branches in some of the valley peat cuttings shows that trees were indigenous here before their comparatively recent reintroduction. These remains are common enough in one of the banks (to the west of Loch Spiggie, Dunrossness) belonging to the writers to be a considerable nuisance when working the peats, and Livingstone (1947) states that a bank had to be abandoned owing to this cause. It is not recorded when this indigenous woodland became extinct: certainly the pre-Norse inhabitants would have made considerable inroads into the supply, and one doubts whether any would have survived the Viking settlement of the ninth century. In the appendix to the famous Orkneyinga Saga (Saga of Olaf, Tryggvi's son, from the *Flateyjarbók*) it merely states: 'Fuel was scarce in the islands'; but Capper (1937, p. 116) goes as far as to say that during Torf Einar's reign: 'The earldom could never be quite free from the need of imports, particularly of timber. And since every foot of wood, even for house-building, had to be brought into the treeless isles....' Torf, or Turf, Einar introduced the using of peat (turf) as fuel into the islands. It is significant, however, that some of the original Shetland place-names contain such old Norse words as Lund (lundr, grove), Vid (viðr, wood) and others: see Jakobsen, 1936, pp. 142–4.

The scattered little groups of trees nowadays are seldom an acre in extent, but Kergord Plantations at the head of Weisdale Voe (six-figure O.S. map reference: 952746)—the subject of the present study—are, for their size, unique in the islands. Their situation is particularly favourable to good growth, being well sheltered in a deep, south-facing valley and having good soil. Dr Edmondston (1809, vol. 1, p. 217) suggested: '...towards the head of Weisdale Voe would, perhaps, be found the most eligible situation for an extensive plantation. The moss there is not deep, the general soil is good, and it lies over limestone.' In spite of this environment it is necessary to be selective in the choice of trees planted there. For example, Japanese larches are growing excellently while European larches are dwarfed and dying. A case in point, too, is given by Raeburn (1888, p. 549) who records that Mr D. D. Black in 1858 planted 40,000 Norway firs on the same estate as that of the present plantations but they all died.

The late Dr Munro started planting trees at Kergord in 1909 and now there are seven plantations grouped around Kergord House, though in fact they might be counted as five, for two 'pairs' are separated only by a narrow road. The two hillside plantations (Lindsay Lee to the south and Leegarth to the north) are almost entirely conifers: the lower ones are well mixed coniferous and deciduous trees. The main valley plantation (Pl. 1) with the roof of Kergord House showing towards the north end, contains, as can be seen, two small fields (one arable, one rye-grass). Excluding these, but including the gardens which have plenty of trees, the total extent of planting is some 8½ to 9 acres. The three dominant species (see list below) are doing well with a good sturdy growth up to 30–35 ft. The lastest foxglove (*Digitalis purpurea*), at the side of the burn running through Lindsay Lee, flowered until early December 1946, which shows the sheltered nature of the situation. In spring the ground is dotted with such typical woodland flowers as primrose (*Primula vulgaris*), wood-sorrel (*Oxalis acetosella*), wood-anemone (*Anemone nemorosa*) and bluebell (*Scilla non-scripta*).

Photo L. S. V. Venables

Photo 1. Kergord: Lindsay Lee above and the House Plantations below.

Photo L. S. V. Venables

Photo 2. Kergord: some of the plantations from the east.

Trees at Kergord Plantations

Dominant (good sturdy growth up to 30–35 ft.):
- Sycamore (*Acer pseudo-platanus*)
- Japanese larch (*Larix kaempferi*)
- Sitka spruce (*Picea sitchensis*)

Less abundant:
- Elder (*Sambucus nigra*)
- *Salix* spp.
- Ash (*Fraxinus excelsior*)
- Rowan (*Sorbus aucuparia*)
- Whitebeam (*S. aria*)
- Alder (*Alnus glutinosa*)
- Horse chestnut (*Aesculus hippo-castanum*)
- Hawthorn (*Crataegus* sp.)
- Silver fir (*Abies alba*)
- *Pinus* spp.
- European larch (*L. decidua*)

} Not doing well

Rare:
- Laburnum (*Laburnum* sp.)
- Daisy-tree (*Olearia* sp.)
- Cherry (*Prunus avium*)
- Sea buckthorn (*Hippophae rhamnoides*)
- Beech (*Fagus sylvatica*)
- Copper beech (*F. sylvatica* var.)
- Apple (*Malus pumila* vars.)
- Holly (*Ilex aquifolium*)
- Cypress (*Cupressus lawsoniana*)
- Chile pine (*Araucaria araucana*)

Secondary growth:
- *Spiraea* sp.
- *Fuchsia* sp.
- Snowberry (*Symphoricarpus albus*)
- *Rosa* spp.
- *Rubus* sp.
- Gorse (*Ulex europaeus*)
- Broom (*Sarothamnus scoparius*)
- *Rhododendron* sp.
- Red currant (*Ribes rubrum*)
- Black currant (*R. nigrum*)
- Flowering currant (*R. sanguineum*)
- Etc.

2. METHODS

As a preliminary to studying the bird population of these plantations we spent a day working out a comprehensive route which would give us a fair chance of a reasonably accurate census of all the birds. Much of the area under trees was open enough for a clear zig-zag walk to present no difficulties, but there were some patches, especially in Lindsay Lee, which were very dense. Through some of these we cut a path, but with others we had to be content with one going right round the edge. Thenceforward the same route was followed on each census tour. The walks were done slowly and silently, and always under the most favourable circumstances—i.e. as early in the morning as possible and never with strong wind or heavy rain. Though complete accuracy is of course not claimed, we do believe that under these conditions very few of the birds escaped being either seen or heard. This method of identification allows the use of trinomials in only a few cases. The study lasted for 2 years: between 9 August 1945 and 21 July 1947, 94 counts were taken at intervals of between 6 and 10 days.

A table was constructed to show the numbers of each species observed on each individual count, and a copy of this has been deposited with the Edward Grey Institute of Field Ornithology, Oxford. Table 1 (published here) gives some of the same data in a reduced form: only those species are included which make a real use of the plantations over a considerable period for cover or as regular feeding or breeding ground. The individual counts for each of these species have been amalgamated to give the average number of birds seen in each month.

3. DISCUSSION OF INDIVIDUAL SPECIES

Some of the more relevant observations on status, distribution and dates for other parts of Shetland are quoted from Saxby and Saxby (1874), abbreviated hereafter to 'Saxby', and Evans & Buckley (1899), the latter abbreviated to E.B. Both are, of course, very much out of date and Saxby's work refers mostly to Unst. Our observations on song- and breeding-dates will be given in a future communication, and are omitted here.

Carrion crow (*Corvus corone*). Two single records in October 1945. This bird, if it was always the same, was seen in the vicinity of Kergord on various dates between 28 September and 8 November. One bird in the plantations on 8 October 1946 and one near them on 23 April 1947. E.B. give only one April record.

Hooded crow (*C. cornix*). In spring a few pairs nested in the plantations, and in winter some roosted in the Lindsay Lee conifers. Other than this, they merely used the trees as convenient perching places and fed outside the woods.

Rook (*C. frugilegus*). One single record in early December 1945 but this bird, if it was always the same, was seen in the vicinity of Kergord on various dates between 28 September and 16 March. It would appear that here the carrion crow is a passage migrant and the rook a winter visitor. E.B. give the rook as irregular in spring, autumn and winter.

Jackdaw (*C. monedula*). Venables & Venables (1947) record the first breeding of jackdaws on Shetland. These few pairs are in or around Kergord and most show the white neck-patch as with the Scandinavian form (*m. monedula*). They are to be seen in the vicinity throughout the year, sometimes in the plantations but more frequently outside.

Starling (*Sturnus vulgaris*). Very fluctuating in numbers and not accurately counted. Flocks or single birds might be in or below the trees one minute and out on the hillside the next. Some roost in the two hill plantations during the winter and some nest in the walls and buildings around Kergord. Presumably all are the local race *zetlandicus*.

Siskin (*Spinus spinus*). Four birds on 18 May 1947.

House-sparrow (*Passer domesticus*). A few nest in the buildings at Kergord and are resident there. They are occasionally to be seen in the plantations; more regularly during spring and early summer.

Table 1. *Monthly averages, to the nearest bird, of the more regular species—excluding hooded crow and starling*

	Aug.		Sept.		Oct.		Nov.		Dec.		Jan.	
	1945	1946	1945	1946	1945	1946	1945	1946	1945	1946	1946	1947
No. of counts ...	3	3	4	5	3	5	3	5	4	4	4	4
Chaffinch	1	—	11	<1	2	13	4	29	2	13	7	14
Goldcrest	—	<1	—	1	1	10	3	7	6	5	5	1
Blackcap	—	1	—	<1	—	—	—	—	—	—	—	—
Song-thrush	8	6	9	6	3	1	<1	—	—	—	—	—
Blackbird	26	22	25	23	12	22	15	20	13	13	12	14
Wren	6	8	5	7	4	4	2	1	2	1	<1	1
Long-eared owl	—	—	—	—	<1	—	—	1	2	2	6	1
Merlin	—	—	—	1	1	<1	1	1	<1	<1	<1	<1
Wood-pigeon	4	1	5	2	4	4	1	2	1	1	—	1

	Feb.		Mar.		Apr.		May		June		July	
	1946	1947	1946	1947	1946	1947	1946	1947	1946	1947	1946	1947
No. of counts ...	3	4	4	4	4	4	4	5	4	4	3	4
Chaffinch	48	1	20	11	1	10	—	<1	—	—	<1	—
Goldcrest	4	—	2	—	2	—	1	—	1	—	<1	—
Blackcap	—	—	—	—	—	—	1	—	3	—	1	<1
Song-thrush	<1	—	<1	<1	2	2	6	4	10	7	7	6
Blackbird	17	12	10	2	12	9	18	12	27	27	23	24
Wren	2	1	2	—	2	—	1	—	<1	—	4	<1
Long-eared owl	7	1	7	1	1	—	<1	—	—	—	(<1)	—
Merlin	—	1	<1	<1	<1	<1	<1	<1	<1	<1	—	—
Wood-pigeon	—	—	<1	—	2	1	2	4	2	4	3	3

Chaffinch (*Fringilla coelebs*). When we visited Kergord on 25 June 1945, before our regular counts began, two chaffinches were heard in song there. Three birds were present when we took our first count on 9 August, but then no more were seen until the autumn flocks arrived on 21 September. Two were singing on 28 March 1946 and a casual bird on 3 July, but there was no attempt at nesting. Next autumn the flocks arrived in early October, and the last of these (30) was seen on 6 April. Song from one of the stragglers was heard by Mr Hunter Sandison on most days between 15 and 29 April, and we saw the last bird (a male) on 12 May. Again there was no attempt at nesting, but the *Handbook* publishes one breeding record near Lerwick. Saxby gives this species as common in winter with a few males in summer, so its status does not seem to have changed over the last 80 years.

Brambling (*F. montifringilla*). In the district as a whole, bramblings are autumn passage-migrants, with a few scattered birds staying on all winter. Mr Hunter Sandison tells us that this is normal at Kergord, too, but neither he nor either of us saw the migrants in the plantations at all during the autumn of 1945. In 1946 flocks were frequent during the month of October and there were a few migrants on the following April. We have some winter records of single birds: usually in stubble fields close to the plantations. Saxby, E.B. and the *Handbook* give the status as autumn and spring passage migrant; but for Kergord and vicinity it is common in autumn with a few in winter and spring.

Mealy redpoll (*Acanthis flammea*). In late October 1945 a flock of 16 was seen at Kergord. At the same period in 1946 small flocks were noted in the vicinity for a week, but none was seen actually in the plantations though a single male was there on 24 November. Winter records for the district are by no means uncommon though we failed to get one at Kergord.

Twite (*A. flavirostris*). Common all over the whole district and not infrequent in the plantations except during winter. A few nest there from just above ground-level up to 14 ft.

Bullfinch (*Pyrrhula pyrrhula*). Occasional single records from November to April: males being in the minority. Both by the plumage and the note we judged all these to be the Northern form (*p. pyrrhula*) with which we are familiar in Lapland. For this form the *Handbook* gives: 'Irregular in autumn and winter' which agrees well with the Kergord observations.

Yellow-bunting (*Emberiza citrinella*). In the winter of 1945–6 a few yellow-hammers appeared in the plantations in early December. Late December and January they spent out in the nearby stubble fields, returning to the plantations for February (highest count—10), with a few lingering on until early March. In the second winter none came to Kergord at all, but we noted a flock of 12 in mid-January in stubble a short way south of the plantations. The *Handbook* says that it is seldom noted on Shetland except on migration; but Mr Hunter Sandison tells us that the 1945–6 observations were typical of most winters for that vicinity.

White wagtail (*Motacilla a. alba*). Locally we have seen them from mid-August to early November but the only plantation record was two on 21 September 1945. The *Handbook* gives it on autumn and spring passage; exceptionally breeding. (Incidentally there was a nest at Lerwick docks in 1946, so far unrecorded.)

Tree-pipit (*Anthus trivialis*). One passage migrant in September and four in May were noted, but this species is easily confused with the next.

Meadow-pipit (*A. pratensis*). Common all round Kergord in spring, summer and autumn, but rare in winter. Sometimes they came into the plantations during late summer and autumn. This seems to be a local idiosyncrasy as Saxby says: 'Often being seen traversing the branches of the trees and shrubs in quest of the numerous insects which resort to them for shelter.'

Goldcrest (*Regulus regulus*). Saxby, E.B. and the *Handbook* give the goldcrest as a regular spring and autumn migrant, but in the plantations it is attempting to establish itself as a wintering species and, possibly, as a breeding bird. In the winter of 1945–6 it managed to survive though in lessening numbers (see Table 1), but during the following year an abnormally severe series of late-December and January gales with sleet storms reduced the population from six in mid-December to three by 1 January and thereafter none. In the first spring (1946) the population was reduced to two birds (a pair?) at about the end of March. Song was commenced by one on 18 February and he kept it up until 22 June, though he had no second bird with him by late April. The same bird, presumably, was occasionally seen until at least 20 September and the first autumn migrants arrived on 1 October. In the second spring (1947) there were, as stated above, no survivors.

Whitethroat (*Sylvia communis*). Spring and autumn migrant throughout Shetland (thus agreeing with the *Handbook*) but, probably by chance, we found it on passage at Kergord only during the autumn. On 29 July 1946, a whitethroat was doing song-flights from a patch of willow scrub at Hellister, to the south of Kergord, and on 29 June 1947, we found a bird doing song-flights from the trees at Sound; also a short distance south of Kergord. It was still there on the next day but had gone by 5 July. On 7 July, however, a bird was singing in the plantations, and the chances are strongly in favour of its being the same one. It was constantly singing from the same place on our last two counts, 13 and 21 July. Saxby records it as an occasional summer straggler and has apparently heard the song.

Lesser whitethroat (*S. curruca*). Recorded for autumn and spring in the *Handbook*. Our only record was a single male, singing loudly, on 22 May 1946. On 14 May 1947, however, there was a singing male in willow trees at Tresta, three miles from Kergord.

Garden warbler (*S. borin*). One record in mid-August, one in mid-September and two (one bird singing) on 1 June.

Blackcap (*S. atricapilla*). The *Handbook* gives it as an autumn and spring migrant, while Saxby records an attempted nest on Unst in a currant bush during early June, but one of the pair was killed 'by an odious cat'. At Kergord it is an autumn and spring migrant but appears to be attempting to establish itself as a local nester. On two casual visits to the plantations on 17 and 25 June 1945, before regular counts had been started, a blackcap was heard singing and on the earlier date the pair was seen carrying nesting material in Lindsay Lee. It is doubtful whether this attempt was successful, because when G. T. Kay and G. W. Russell revisited the place in early July they found no trace of the birds. In 1946 three singing males established themselves in the plantations in late May, and full song was heard, usually from all three, until 11 July. One was singing quietly on 21 July and one was giving occasional sub-song on 1 August. Unfortunately, none of these males managed to get a female. In the second spring (1947) no migrants were seen, but a singing male appeared during late June in Lindsay Lee and sang until at least 7 July.†

Barred warbler (*S. nisoria*). In parts of Shetland, e.g. Lerwick and Fair Isle, this is a fairly common autumn migrant. The *Handbook* gives it also in spring. At Kergord we had only one September record.

Willow warbler (*Phylloscopus trochilus*). At Kergord during our two years this bird was regular in autumn with a few in spring. Two were heard singing on 21 September 1945. Both *t. trochilus* and *t. acredula* were seen, but a familiarity with these two variable

† *Addendum.* In mid-July 1948 a pair of blackcaps was feeding young in the nest in Lindsay Lee.

forms in England and Lapland has shown us how unsafe it is to split them by sight identification sufficiently accurately to give comparative figures.

Chiffchaff (*P. collybita*). A few in spring and a regular autumn passage bird in September. After this month various single birds wandered through, showing considerable plumage variation though all were attributable to *collybita* owing to their blackish tarsi. On 11 and 21 November 1945 and 22 October 1946 a bright yellow chiffchaff was present—considerably brighter than any British breeding bird we have seen. The call-note was characteristic, too, being the typical *phylloscopus* '*hweet*' or '*hooeet*', but noticeably more sibilant, curtailed and quiet than with the British form. On 27 October 1946 there was a chiffchaff with outstandingly dull plumage: a brownish bird, darker above and more buffy below, but with not the slightest trace of white or yellow. No call was heard. On 13 and 24 November and 1 December 1946, a probable Siberian chiffchaff (*tristis*) was in and around the gardens. It did not give its call-note, said to be diagnostic, but the distinctive plumage and the Shetland dates as given in the *Handbook* all point to its being of this form.

Mistle-thrush (*Turdus viscivorus*). One September passage migrant.

Song-thrush (*T. ericetorum*). Is definitely on the increase in Shetland and is now breeding where there is suitable cover of trees or bushes. Saxby gives only one occurrence (no date) and E.B. have a few definite records, all in summer and autumn around the 1890's. The *Handbook* gives it as 'scarce, though increasing (considered to be the Continental form)'. We cannot be dogmatic as to the race breeding at Kergord, for we have collected none, but the back colour of these birds appears to be typical of the British form (*e. ericetorum*), while the few winter visitors have the greyer backs of Continentals (*e. philomelus*).

The breeding birds arrive during late March and April, leaving again during late September and October. The earliest nest had *c*/4 completed on 16 or 17 April, and the latest nest hatched *c*/4 on about 30 July. Some, at least, are double brooded but the figures in Table 1 show the highest counts around early June when most of the young are leaving the nests. As has been stated above, an occasional greyer-backed thrush turns up in the winter.

Redwing (*T. musicus*). A scarce passage migrant in the first autumn but plentiful in the second: Mr Hunter Sandison assures us that the second autumn was the typical one—highest counts 30, 40 and 42. Occasional birds are seen at Kergord or in the locality right throughout the winter, and we have noted that every time a good view of these has been obtained they have had the darker coloration of the Iceland form (*coburni*), a bird with which we are familiar on the breeding grounds. Though this sight-splitting of geographic races is very misleading, nevertheless, a dead redwing that we picked up in the south-east plantation on 8 March was a definite *coburni* with a wing of 123 mm. The *Handbook* gives this form as a winter visitor to Shetland.

Fieldfare (*T. pilaris*). As with the redwing, fieldfares almost missed Kergord in the first autumn but were more typically common in the second—highest counts 20, 30 and 150. On rare occasions we saw one or two birds in the locality during the winter. Saxby said that it had a spring migration through Unst, and we saw one bird in the plantations on 6 May.

Blackbird (*T. merula*). This species has increased considerably on Shetland in recent times. It may now be said to breed almost anywhere where there are bushes and, in some cases, right away from cover of that sort; nesting in heather or stone walls and singing from buildings, walls or rocks. Lack (1942*b*) records a similar practice in Orkney and we have seen it on such places as Ailsa Craig and, indeed, not so very rarely in England. In Saxby's time the blackbird was a common migrant in spring and autumn with a few males remaining throughout the winter. Nesting was attempted in his garden on Unst, but was always defeated by his numerous cats. He says, however, that: 'There is little doubt that it has bred in the southern districts.' E.B. give it as a not very common spring and autumn migrant with a few wintering, and record rare breeding occurrences from 1888 onwards. The *Handbook* says it is a local nester.

Nowadays it breeds commonly at Kergord, and some spend all the winter in the plantations. There is also an autumn passage which was very marked during early November 1946. The Turdidae migration was a particularly good one on that autumn, when all through late October and early November flocks, sometimes several hundred strong, of redwings, fieldfares with some blackbirds were scattered throughout the hills. This is reflected in Fig. 1.

Our earliest Kergord nest was 19 April (incubation) and our latest was young being fed in the nest on 3 July. Some, at least, are double brooded and the figures in Table 1 and Fig. 1 show the highest summer counts starting around June when most of the young are leaving the nest. In 1946 the blackbirds started singing on 25–26 March, and it was noted that between the counts of 15 and 28 March they had ceased being a loose flock round the home plantations and were much more scattered throughout the woods—an indication of when breeding territories are claimed.

Many of the breeding population leave with the autumn passage birds but some remain all the winter. Saxby says: 'In the month of October they arrive in small but distinct flocks, the number of males exceeding that of the females by about one-third.' As mentioned above, he says that a few males remain throughout the winter. Our impression for the main-

land of Shetland as a whole is that there is a considerable drop in the blackbird population during the winter, and that there are then many more males than females. So far, the only quantitative data we have to support this latter point is that between 21 November 1947 and 31 January 1948, of the 44 blackbirds seen in Dunrossness (every effort being made to eliminate recounts of local residents) 14 (32 %) were adult males, 26 (59 %) immature males and 4 (9 %) females. This study is being continued. During the winter of 1946–7 approximately 13 blackbirds remained at Kergord and on 1 January most of the morning was spent in getting a good view of these 13 individuals in bright sunlight. The results also showed a preponderance of males:

Adult males	7
Immature males	2
Females	4

impression of the robin's status on Shetland. They are regular autumn migrants in small numbers (spring migration, too, is recorded by E.B.), and a few winter in gardens with plenty of cover. The *Handbook* gives the Continental form (*r. rubecula*) as being the wintering race for the northern isles, and such views as we have had of the backs and breasts (lighter tinted than with *r. melophilus*) of winter birds substantiate this.

Wheatear (*Oenanthe oenanthe*). A common breeding bird on the hills around Kergord, and occasionally occurs among the trees in early autumn and late spring: probably passage birds.

Hedge-sparrow (*Prunella modularis*). One 22 April record.

Wren (*Troglodytes troglodytes*). Even though we have found only three (two unoccupied) nests actually inside the plantations—all against the trunks of Sitka spruces—wrens were noted on practically every visit

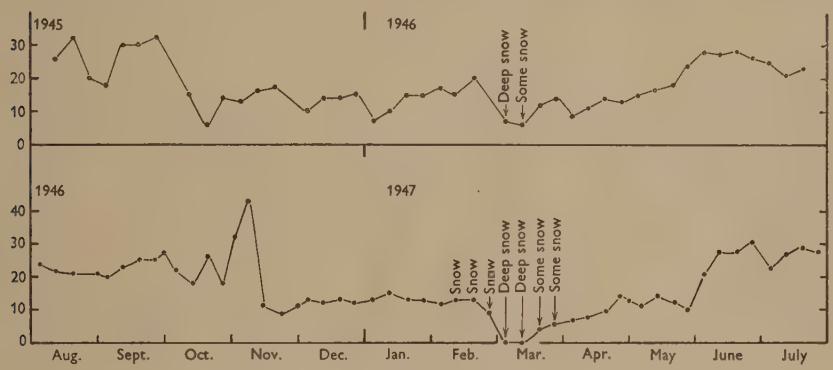


Fig. 1. Actual numbers of blackbirds counted at Kergord.

In the second winter (1946–7) there was deep snow covering all the ground from 22 February to about 15 March: the worst year for hill-sheep in living memory. All the blackbirds forsook the plantations for local stackyards and middens round the byres. Males returned before females as follows:

20 March	4 males	0 females
26 March	6 ,,	0 ,,
1 April	6 ,,	1 ,,
6 April	6 ,,	2 ,,

and song had started by our 13 April visit. Though song was later in commencing after this severe winter (dawn song would not, of course, have been heard), the return to territory was not much delayed, but the melting of the snow was opportune for this.

Redstart (*Phoenicurus phoenicurus*). A few on passage; spring and autumn.

Robin (*Erithacus rubecula*). The few single records for Kergord in September and March give a false

(10 being the highest count) until the deep snow of the second winter. There were a fair number of survivors in the district, which had weathered it out in the farmyards and on the intertidal, but none returned to the woods until our last census on 21 July 1947 when a single bird was there. Presumably all are the local race *zetlandicus*.

Pied flycatcher (*Ficedula hypoleuca*). A few in September and May.

Barn owl (*Tyto alba*). A very rare Shetland visitor: not mentioned in Saxby and given square brackets in E.B. The *Handbook* gives one February record for the white-breasted form (*a. alba*) and one November record for the dark-breasted form (*guttata*). In early December 1945, there was a small movement of barn owls through the plantations. On three consecutive counts we observed: 1 December, two dark breasted; 9 December, four dark breasted and one light breasted; 15 December, one dark breasted. None was seen during the second winter.

Long-eared owl (*Asio otus*). Saxby gives a few winter records as do E.B. who also say: 'Observed on migration in most years'. The *Handbook* gives it as an uncommon migrant. In 1935 Mr Hunter Sandison found an incubating bird of this species on an old crow's nest in the home plantations at Kergord from which three young successfully flew. It will be seen in Table 1 that they wintered in the first year (1945–6) of our observations in fair numbers, but there was no attempt at breeding in the spring, in spite of records, until early May (Mr R. Henry saw two on 25 July 1946). In the second year a few started wintering, but the numbers were reduced during the bad gales (see goldcrest), and the last survivor was found dead at the end of the period of deep snow (see blackbird). This proved to be a remarkably big bird with wing measurement of 302 mm.

Table 2. *Numbers of Blackbirds*

1945.	Aug.	9	26	1946.	Sept.	7	20
		15	33			14	23
		26	20			20	25
	Sept.	3	18			26	25
		12	30		Oct.	1	27
		21	30			8	22
		28	32			14	18
	Oct.	10	15			22	26
		18	6			27	18
		27	14		Nov.	1	32
	Nov.	2	13			7	38
		11	16			13	11
		21	17			19	9
	Dec.	1	10			24	11
		9	14		Dec.	1	13
		15	14			7	12
		22	15			14	13
1946.	Jan.	1	7			22	12
		8	10	1947.	Jan.	1	13
		14	15			13	15
		24	15			20	13
	Feb.	2	17			25	13
		12	15		Feb.	1	12
		18	20			7	13
	Mar.	2	7			14	13
		8	6			21	9
		15	12		Mar.	5	—
		28	14			13	—
	Apr.	5	9			20	4
		9	11			26	6
		16	14		Apr.	1	7
		22	13			6	8
	May	1	15			13	9
		7	16			22	14
		16	18		May	1	13
		22	24			6	11
	June	1	28			12	14
		9	27			18	12
		15	28			25	10
		22	26		June	1	21
	July	3	25			7	28
		11	21			14	28
		21	23			25	31
	Aug.	1	24		July	1	23
		8	22			7	27
		15	21			13	29
	Sept.	1	21			21	27

They never leave the home plantations, no doubt owing to the presence of house-mice (*Mus musculus*) at the buildings and small oat-ricks. We have pulled apart many castings and have found them to be composed of house-mouse remains with an occasional bird bone—probably of the starling.

Sparrow-hawk (*Accipiter nisus*). Rare migrant (*Handbook*). A female was in Lindsay Lee on 9 and 15 June 1946. She had apparently been wounded but was well on the way to recovery on the second date.

Merlin (*Falco columbarius*). Though these birds nest away up in the hills they are definitely attracted by the Kergord trees and are frequently to be seen hunting in and around them. At least four were shot in the plantations during our first year's observations. We have records of merlins eating the following birds in or immediately outside the plantations:

February	Blackbird, jackdaw.
March	Blackbird, chaffinch, snow-bunting.
April	Starling.
October	Redwing.
November	Unsuccessful stoop at wood-pigeon.
December	Blackbird.

Woodcock (*Scolopax rusticola*). A fairly common migrant and winter visitor on the hills of Shetland. This is a species that can easily be overlooked in woodland, which no doubt accounts for the fact that we have only a few records for Kergord: in November, February and March. They were all during the second year which was, in general, a better year for woodcock up in the hills.

Wood-pigeon (*Columba palumbus*). This bird has succeeded in establishing itself, in a small way, in the plantations. Saxby gives it as a spring and autumn migrant in small numbers, E.B. a few records from spring to November, and the *Handbook* as a passage migrant. A few pairs bred successfully at Kergord on each year of our observations (1945–7), but Mr Hunter Sandison says that they started some years prior to this. In both autumns some pigeons started to winter there but, what with being shot in the surrounding rickyards and kaleyards, together with the severe weather during the second winter, none managed to survive right through (see Table 1) and there was an hiatus until the April migrants arrived.

Birds outside the plantations

The following is a list of birds seen, in some cases frequently, immediately outside the plantations but never inside:

Raven (*Corvus corax*).
Corn-bunting (*Emberiza calandra*).
Snow-bunting (*Plectrophenax nivalis*).
Skylark (*Alauda arvensis*).
Peregrine (*Falco peregrinus*).
Swallow (*Hirundo rustica*).
Gull (*Larus* spp.).
Rock-dove (*Columba livia*).
Snipe (*Capella gallinago*). One dead inside during winter.
Cuckoo (*Cuculus canorus*). One calling near Lindsay Lee from mid-May to mid-June 1947.

Migrants south of the plantations

During the two years' study of Kergord we were living in the same valley in which the plantations are situated but 3½ miles farther south. The following is a list of migrants, other than species already mentioned, seen in and around our garden, and which must have passed through or near the plantations when higher up the valley:

Lapland bunting (*Calcarius lapponicus*), August–September.
Waxwing (*Bombycilla garrulus*), November.
Short-eared owl (*Asio flammeus*), May and October.
Water-rail (*Rallus aquaticus*), October.
Turtle-dove (*Streptopelia turtur*), September.
Swift (*Micropus apus*), June.
House-martin (*Delichon urbica*), spring and autumn.
Wryneck (*Jynx torquilla*), May.

Mammals in the plantations

Cat (*Felis domesticus*). Few—semi-wild.
Stoat (*Mustela erminea*). Two records.
Otter (*Lutra lutra*). One in Lindsay Lee on 1 September 1946.
House-mouse (*Mus musculus*). Common around the home plantations.
Rabbit (*Oryctolagus cuniculus*). Some—in deep snow even conifers were being ring-barked.

Though sheep sometimes get into the plantations the fences are sufficient to keep out the Shetland ponies.

4. GENERAL DISCUSSION

It appears from these records that Kergord plantations have influenced the status of several birds, hitherto usually regarded as passage migrants in Shetland. This considerable area of woodland lies in close proximity to farm buildings with associated crops, corn-ricks, mice, middens, etc., so providing both cover and food supply. These factors have enabled some species to stay and breed (notably wood-pigeon and jackdaw, though long-eared owl, goldcrest and blackcap are apparently making the attempt), and have encouraged others to remain throughout the winter.

By reason of its heavy gales and snow, Shetland is not a very suitable wintering ground for many birds, but Kergord can provide an adequate environment for some species which do not normally remain in Shetland, though it appears to be very close to the border line. Thus yellow-bunting, long-eared owl and goldcrest survived there during the winter of 1945–6 but not in the following winter of prolonged snow. Wood-pigeons, if they were not shot, would almost certainly survive. The winter also sees a small resident population of blackbirds, wrens and hooded crows, together with flocks of chaffinches and an occasional redwing, fieldfare and woodcock. The occurrence of occasional bramblings and yellow-buntings seems due to the presence of the plantations, for we have not seen them at this season in other parts of Shetland.

April is a month of change. Purely winter species are disappearing to give place to incoming migrants such as song-thrush, wood-pigeon and extra blackbirds which settle down to breed, so increasing the population further. (The gradual build-up of numbers can be well seen in Fig. 1, relating to blackbird only.) Some species which winter outside the plantations return thither in the breeding season and appeared regularly on the summer counts, e.g. jackdaw and twite. Yet another group includes those species which remain for part of the summer, apparently disposed to breed though never achieving this end: of these the goldcrest, chaffinch and long-eared owl represent survivors from the winter population, while others, such as blackcap and whitethroat, come with the northward migration. Purely passage birds are comparatively rare during the spring movement but some of these stop for a while as though trying out the habitat for a breeding ground.

The bird population reaches its maximum in September and October, when the summer species are augmented both in numbers and kinds by autumn migrants on passage. These may visit the plantations in considerable numbers though, by virtue of its central position, Kergord is not so well situated for migrants as the coastal districts of Shetland.

The population here has other enemies 'save winter and rough weather'. Merlins breed regularly in the hills and one or two of these were frequently seen in the plantations throughout the year. The long-eared owls probably took slight toll of small passerines, though pellet analysis showed their chief food to be house-mice. Several feral cats also hunted the locality; and wood-pigeons were shot by man. More subtle human intervention may also be noted: since the end of the war the returning laird has instituted many changes such as thinning some of the cover, clearing the neglected main garden of brush-

wood and removing the lower branches from many trees and bushes. It remains to be seen whether or not these changes will prove detrimental to the wild population here considered.

5. SUMMARY

1. By far the largest area of woodland on Shetland is at Kergord, Weisdale, where some 8 to 9 acres of mixed plantations are growing well. Between August 1945 and July 1947 the writers took 94 counts of the birds there: the results are discussed above and the complete, tabulated counts deposited with the Edward Grey Institute of Field Ornithology, Oxford.

2. It was found that these plantations have influenced the status of some of the birds usually regarded as passage migrants on Shetland. Among these are jackdaw (*Corvus monedula*), breeding; goldcrest (*Regulus regulus*), wintering and possibly attempting to breed; yellow-bunting (*Emberiza citrinella*), wintering; blackcap (*Sylvia atricapilla*), apparently attempting to breed; long-eared owl (*Asio otus*), wintering and one breeding record; and wood-pigeon (*Columba palumbus*), breeding and endeavouring to become resident.

3. Both the song-thrush (*Turdus ericetorum*) and the blackbird (*T. merula*) are becoming commoner as breeding species on Shetland. A graph is given of the absolute numbers of blackbirds seen on every count, and the preponderance of males in the wintering population is discussed.

4. The history of the plantations with a list of the tree species, a list of the mammals noted there, together with other relevant facts are also given.

6. ACKNOWLEDGEMENTS

To Major and Mrs Winton of Kergord House who gave us the freedom of their plantations and gardens. To Mr R. Henry and Mr Hunter Sandison of Kergord Estate who gave us considerable help.

REFERENCES

(General references are marked with an asterisk)

Capper, D. P. (1937). 'The Vikings of Britain.' London.

Edmondston, A. (1809). 'A view of the ancient and present state of the Zetland Isles....' Edinburgh. 2 vols.

***Evans, A. H. & Buckley, T. E. (1899).** 'A vertebrate fauna of the Shetland Islands.' Edinburgh. (Covers most of Shetland but a large number of the observations are secondhand.)

Jakobsen, J. (1936). 'The Place-names of Shetland.' London and Copenhagen.

Lack, D. (1942*a*). 'Ecological features of the bird faunas of British small islands.' J. Anim. Ecol. 11: 9–36.

Lack, D. (1942*b*). 'The breeding birds of Orkney.' Ibis, Ser. 14, 6: 461–84; (1943), 85: 1–27.

***Lack, D. & Venables, L. S. V. (1939).** 'The habitat distribution of British woodland birds.' J. Anim. Ecol. 8: 39–71.

Livingstone, W. P. (1947). 'Shetland and the Shetlanders.' London.

MacDiarmid, H. (1939). 'The islands of Scotland.' London.

Raeburn, H. (1888). 'The summer birds of Shetland, with notes on their distribution, nesting, and numbers.' Proc. Roy. Soc. Edinburgh, 9: 542–62.

***Saxby, H. L. & Saxby, S. H. (1874).** 'The birds of Shetland with observations on their habits, migration, and occasional appearance.' Edinburgh. (Mostly concerned with Unst.)

Venables, L. S. V. & Venables, U. M. (1947). 'Jackdaws Breeding in the Shetland Isles.' Brit. Birds, 40: 140–2.

***Witherby, H. F., Jourdain, F. C. R., Ticehurst, N. F. & Tucker, B. W. (1938–41).** 'The handbook of British birds.' London. 5 vols.

THE MEANING OF PRODUCTIVITY IN BIOLOGICAL SYSTEMS

By A. MACFADYEN, *Bureau of Animal Population, Oxford*

(With 1 Figure in the Text)

1. INTRODUCTION

The growth of the study of living communities as organic systems in their own right, possessing characteristics which are not to be predicted from the behaviour of their constituent individual organisms, is resulting in the development of a new terminology. The description of the structure of communities is based on competition between organisms feeding on the same resources and on the 'layering' of the community which results from the feeding habits of different species, and is represented by the now familiar 'Eltonian Pyramid'. The quantitative relationships of such a system and the relative significance of the different species represented in it are most easily traced by measuring the flow of energy and matter through the constituent organisms, and it is in connexion with this aspect of community studies that the terms 'production', 'productivity' and 'yield' have been given special technical meanings. As we shall see, authors have not always been aware of, or at least have not always observed, the precise meaning attached to these words by their predecessors and it is with the intention of drawing up a 'table of synonymy' rather than that of adding yet further to an ever-expanding jargon, that these notes have been compiled. At the same time it is proposed to investigate the meaning of these words and attempt to relate them to characteristics of living systems encountered in practice.

2. DEFINITIONS OF PREVIOUS AUTHORS

(Refer throughout this section to Table 1)

With the exception of an extremely general definition of 'specific productivity' by Lotka (1925), the first modern author to attempt a critical assessment of the use of these terms was probably Thienemann (1931). Thienemann distinguished the following uses of the word 'production':

(1) The dictionary definition, meaning the *process* of production, that is, gathering or manufacture of material. This definition is not used in biology.

(2) The quantity of that which is produced, i.e. quantity of matter derived (usually by man) from a given area or biological community. 'Productivity' is the rate at which this quantity of matter is accumulated.

(3) He considered that modern biologists use the term 'production' to mean 'the amount of organic matter produced in a given time from organisms and their excreta' but considered that this quantity is not susceptible to measurement in practice because of the difficulties inherent in making such measurements with organisms which have more than one life-cycle in a year and because of the continuity of the process from one year to the next.

It seems evident that most biologists have a 'common sense' idea of the meaning of 'productivity' in this last sense of Thienemann which is akin to that of the 'richness' of a habitat, but that Thienemann's assertion about the impossibility of measuring 'productivity' has gained such wide acceptance that it has come to be regarded as one of those nebulous terms coined by theoretical biologists which are of no practical applicability or interest. It is hoped to demonstrate during the course of this paper that Thienemann's difficulty is based on a fundamental confusion of matter and energy in living systems, and that this property of organic systems is indeed susceptible of precise definition and of measurement.

It is important to realize that biological communities differ fundamentally in one respect from, for instance, chemical systems, as regards the application of the term 'yield'. In the case of the chemical reactions a completed process with an 'absolute' yield is usually involved, whereas in biological communities, because processes such as we are considering are continuous in time, the time element cannot be eliminated from consideration. Thus a yield per annum is a rate of yield. When, however, a yield is defined as the difference between two quantities at different times this does imply a quantity Q and not a rate.

Although in Thienemann's second definition, production is a 'quantity of matter', the third definition brings in 'quantity of matter per annum' which is a rate. Let us denote quantity of matter by Q and time by T, then the two definitions include the components Q and Q/T respectively. This means that 'productivity' in Thienemann's second definition is equivalent to 'production' in his third, from this point of view. It might be debated whether 'productivity' is best denoted by Q/T or by dQ/dT, but a very brief consideration of his paper will show that he was not, in fact, concerned with instantaneous rates and that Q/T, denoting the 'production' in a finite period of time, is the appropriate symbolism.

Tansley (1929) defined 'productivity' as a 'rate of production', where his use of the words is evidently in conformity with Thienemann's second definition; Tansley pointed out that the term may be applied to each food group in the ecosystem, so that the productivity of the herbivore group, for instance, is the rate of production of food matter by that level, in other words, the rate of *consumption* of plant matter.

Borutzky (1939*a*, *b*), in a most ambitious but necessarily rather cursory investigation, estimated the 'productivity' of the Diptera, and especially of *Chironomus plumosus* in various lakes. He estimated the biomass present in each stage of the life history and throughout the year by quantitative sampling methods, and also the growth, birth and mortality rates. He used the words 'productivity' and 'production' synonymously (as far as can be judged from the English summary to his paper) as meaning the peak biomass present, minus that at the beginning of the year (which is the 'resting phase' when the lakes are iced over). In other words, productivity is a difference in quantity of matter, or 'Q' of our symbolism, and represents the total quantity of biomass returned to the lake as food for predators, scavengers, etc. in one year, if the biomass of living larvae is the same in the early spring in the two consecutive years under consideration. This yearly quantity is evidently dimensionally equivalent to Tansley's 'productivity', but differs in that it does not account for the food consumed and wasted in conversion to energy by the flies themselves.

Windberg & Iarovitzina (1939) use the term 'primary production' to mean the 'total quantity of organic matter newly formed in the process of photosynthesis'. If one adds to this definition the words 'per annum', which are evidently implied, it comes into line with that of Tansley, except that it is restricted to the plant level by the addition of the word 'primary'. This is because the biomass created by photosynthesis is the total intake by the plants.

Harvey (1942) reproduces this view, in reference to the sea, in defining the 'production' of a body of water as 'the quantity of organic matter produced by the phytoplankton over a period of time, such as a year'.

Palmgren (1942) writes of the 'productivity' of forests as meaning the total timber yield per annum; thus he is using the word in basically the same way as Tansley and others, but is restricting its meaning to the human level in regard to man's 'herbivorous' activities in exploiting trees, not for food in this case. It is the 'primary productivity' of Windberg & Iarovitzina in this very special sense.

Lindeman (1942) and Hutchinson (1942) use their terms in the same way and can be treated together. Lindeman defines 'productivity' as the rate of flow of energy into the organisms of a given trophic level, that is the annual ration of calories of the organisms of a level, where the 'trophic level' consists of those organisms which derive their nutriment from the same type of food resource, for example, herbivores, primary carnivores, etc. Lindeman makes it clear, despite the definition just given, that he is not concerned with instantaneous rates of energy flow, but with mean rates, and he quotes Hutchinson as saying 'in practice it is necessary to use mean rates over finite periods of time as approximations to true mean rates'. This is expressed in his equation

$$\frac{d\Lambda n}{dt} = \lambda_n + \lambda n',$$

where Λ_n = energy content of trophic level n, λ_n = productivity or 'rate of production' in which λ_n is negative and $\lambda_{n'}$ positive.

Using notation, comparable to that which we have used so far, we can signify energy by E and 'productivity' as defined by Lindeman by $\delta E/\delta T$. Lindeman defines Λ_n or 'energy content of the nth trophic level, uncorrected for dissipation of energy by respiration, predation or death' as the 'yield' of that level. That is to say 'yield' is the summation of all the

Table 1. *Summary of definitions of the words 'production', 'productivity' and 'yield' as used by the authors mentioned*

Author	Production	Productivity	Yield
Thienemann (2)	Q	Q/T	—
Thienemann (3)	Q/T	—	—
Tansley	Q	Q/T	—
Borutzky	Q/T	Q/T	—
Windberg & Iarovitzina	Q/T*	—	—
Harvey, Palmgren	Q/T*	Q/T*	—
Lindeman	Q	$Q/T\ (dQ/dT)$	$Q = \Sigma \frac{QT}{T}\left[\int \frac{dQ}{dt}\,dt\right]$
Ivlev	Q/T	Q/T*	—
Clarke, Ricker	—	'Production rate' Q/T	Q/T*

* Signifies that the use of the term is restricted to a single organism or group of organisms.

productivity over a period of time and is also the difference of two energy contents or, in our symbols, 'E'.

It will be noted that Lindeman uses the differential but we have avoided doing so; in the first case 'yield' is (dE/dt) and in the second it is E/T.

Lindeman's use of the term 'yield' is essentially similar from the dimensional point of view to Thienemann's use of the word production in his second definition, in that both refer to quantities and neither to rates.

Since Lindeman defined 'productivity' as 'rate of production', production itself should be a *quantity* of energy E, which is consistent with its other definition as a difference between two yields (also E). Lindeman makes use of various constants calculated by Juday (see Lindeman, 1941) to convert figures for biomass to energy content; for the purposes of the present argument and for reasons considered below it is permissible to substitute 'Q' for 'E' in the above definitions because he is simply using biomass figures multiplied by constants dependent on the food in question. This gives definitions for productivity as $\delta Q/\delta T$ (dimensionally equivalent to Q/T) and for production as Q and yield as $\Sigma\ (\delta Q/\delta T)$ (dimensionally equivalent to Q).

Ivlev, a translation of whose work was most kindly given to the Bureau of Animal Population library by Dr W. E. Ricker, criticizes Lindeman's interpretation on the grounds that derivation of food from levels other than those immediately 'inferior' is, in practice, so common that the 'trophic level' concept is an unjustifiable over-simplification and that each individual species should be considered separately on its own merits. However, in view of the admittedly theoretical nature of this type of discussion and the fact that one can almost invariably construct relatively simple 'food chain' diagrams and classify their component organisms into 'plants', 'herbivores', 'primary carnivores' and so on, Ivlev's objection seems somewhat misplaced. It is evident that such discrepancies as exist could be readily accounted for by greater elaboration. Ivlev draws attention to the fact that the majority of food supplies are exploited by small numbers of overwhelmingly important organisms and that food chain diagrams can thus often be simplified. He himself uses 'production' to mean 'productivity' (in Tansley's sense) for each species and the word 'productivity' in Palmgren's anthropocentric sense as the annual yield of fish or other product of economic interest.

Ivlev's introduction of the term 'ectrophic coefficient', to express the 'predatory efficiency' of an organism, does not prevent his treatment from being fundamentally similar to that of previous workers.

Clarke (1946) and Ricker (1946) use the term 'gross production rate' to mean the rate of assimilation shown by organisms of a given trophic level, that is Q/T (Lindeman's 'corrected productivity'); and 'net production rate' (Lindeman's 'uncorrected productivity') they use to mean the assimilation rate, less the rate of loss of matter by predation, respiration and decomposition. They avoid the use of the word 'productivity' altogether, but their term 'production rate' evidently means the same. They use the term 'yield' in the sense in which Ivlev and Palmgren use 'productivity', namely as the gross 'productivity' of man as predator on a crop of economic importance—in this case, fish.

Ivlev's (1945) paper contains a further review of previous uses of these terms, showing even greater discrepancies in their meaning, but a table summarizing simply the dimensional components of the terms as used by the above authors will, perhaps, suffice to show how great is the disagreement between them (Table 1).

It seems evident that the most generally accepted use of the term 'productivity' is as a rate of flow of matter or Q/T, although Clarke and Ricker prefer 'production rate', and Lindeman himself uses the differential in his equations, although apparently not meaning it in his writing. It would seem that the other fundamental concept is that of a simple quantity of matter. The term 'production' is defined so variously that its use should be abandoned; but 'yield' is, perhaps, available for use in this sense, following the precedent of Lindeman, unless it is felt that the anthropocentric associations of the word are already too strong.

3. 'PRODUCTIVITY' AND THE MEANING OF 'MATTER' AND 'ENERGY' IN BIOLOGICAL SYSTEMS

In fact, when communities or ecosystems are being investigated, measurements are usually made in terms of numbers of individual organisms in the first place. By multiplying these figures by the mean weights of the species a figure for quantity of living matter or 'biomass' is obtained, which is used for comparison between the different 'trophic levels'. It has often been urged that this is only a rough measure in view of the variable quantities of inorganic substances present in different types of organisms. It has, therefore, been suggested that the 'biomass' of each type of food organism should be multiplied by a specific calorific value so as to give a comparable measure of the energy contents of the different levels, as is done, for example, by Lindeman (1941).

However, in practice, we rarely know the calorific values by which to multiply the biomass figures and, as a first approximation, these are assumed equal for all organisms so that, when considering the whole

ecosystem, it is assumed that the biomass and energy values will give essentially the same relative importance to each group of organisms. However, Bornebusch (1930) has shown that this is far from being the case in forest soils, and the available figures for fresh-water organisms point in the same direction. The ready conversion of biomass to energy figures, and the indiscriminate use of the terms as used by the American authors, would seem to have led to the obscuring of the fact that the energy and biomass cycles are fundamentally distinct and of a different nature, as is shown by Fig. 1, which is a greatly oversimplified diagram of the matter and energy relations of a completely isolated living system, showing no tendency to 'evolution'—in the limnologists' sense. *Whereas energy passes only once through an ecosystem and is utilized only by one animal on one occasion, matter is continuously either circulating or in store; it does not leave the system* (*by definition*). This circulation of matter, often many times in a year, was the cause of Thienemann's dilemma; but when it is appreciated that the matter can be regarded as a 'vehicle' for the energy, originally derived from the sun, in the same way as, in the simple analogy, electric 'charges' can be regarded as the constantly circulating vehicles for electrical energy in a circuit, a solution to this dilemma is at once apparent. The photosynthetic processes of the plants raise the energy levels of the matter they contain, which matter is then circulated through the system, first by way of the plant's own metabolic processes and then through those of the other members of the food chain; at some stage in this flow any given 'quantum' of energy will be dissipated by some organism and will thus be lost to the system, while the 'degraded' matter eventually finds its way back to the plants to be re-charged with energy once more. (Of course this is only broadly true as, not only is matter lost to systems, but in a given organism energy may be transferred from one substance to another; however, the general conclusions remain valid.)

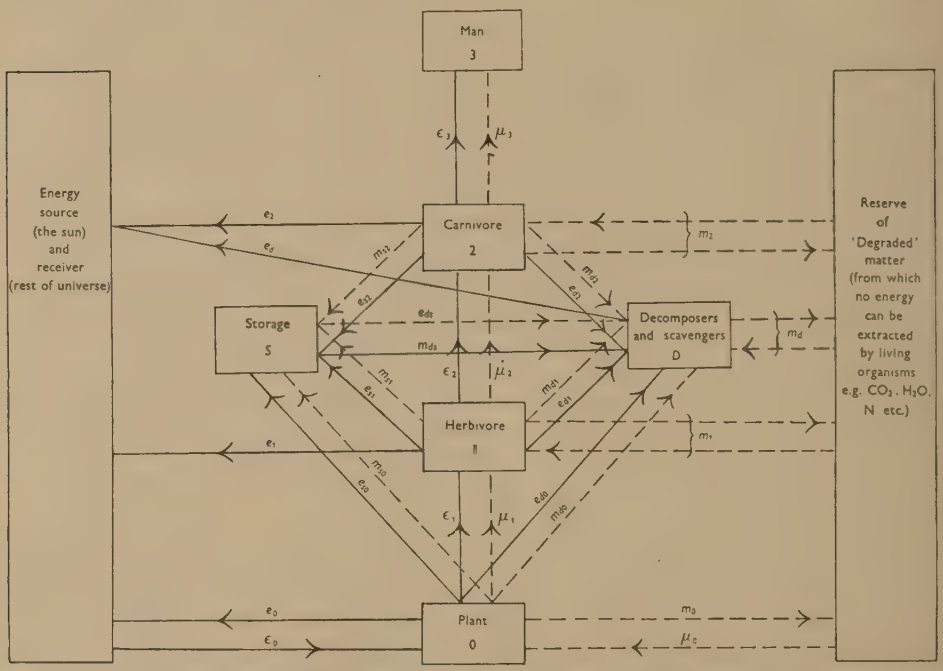


Fig. 1. A diagram to illustrate the relationships between the cycles of matter and of energy in a very simple biological system. - - - - matter cycle, ——— energy cycle, ϵ = 'production' in terms of energy, μ = 'production' in terms of matter, e = energy output by respiration, e_d = energy output by decay, e_s = energy output by storage, m = excess output of 'degraded' matter, m_d = matter in decay, m_s = matter in storage.

One result of the confusion between the two cycles is exemplified by Clarke's remark that, in order to measure the production rate of a community, we

cannot simply measure the energy or the biomass flow (the words are used synonymously) in the various levels and sum them because 'material and energy are used again and again by successive trophic levels'. The material *is* 'used' again and again, but the energy is *not*; once it has been converted into heat by a given individual it is lost to the ecosystem (except for a quite negligible heating effect of one organism by a second). It follows that Clarke's corollary applies only to matter; whilst it is true that one cannot sum the matter in circulation because it circulates to a variable and unpredictable extent, one certainly can sum the energy flow through it. Indeed a measure of this rate of energy flow would seem to be the obvious measure of the activity or 'richness' of such a system and thus to supply the means of solving Thienemann's dilemma and giving a precise meaning to the 'common sense' idea of 'productivity'. However, this word has acquired a different and technical meaning, and we require a new word to signify the total flow of energy in calories per unit time through a system. For present purposes the word 'activity' will suffice. It will be evident from the figure that the energy 'stream' can be measured either at its outflow as the total of $e_1+e_2+e_d$ produced in respiration and returned as heat to the outer universe; or, alternatively, it can be measured at its entry into the system as the rate of production of organic matter by photosynthesis divided by the correct calorific values. It is doubtless in an attempt to express this concept that Windberg & Iarovitzina, and later Harvey, formulated their definitions of 'productivity' and 'production' respectively.

Provided that the system is a stable one in which the matter reservoir is not changing, the two quantities. 'energy output rate' and 'energy input rate' should equate and be equal to the 'activity' which we are seeking to measure. If there were no animals present to feed on the plants and so to make 'degraded' matter available to the plants once more, the rate of flow of energy would be automatically slowed down until production of 'energized' matter were balanced by the processes of decay. The net result would be a slower rate of utilization of the sun's energy and a lower level of 'activity' in the system.

In other words, our 'activity' is in some way descriptive of the overall power of utilizing the sun's energy and producing biological activity in an ecosystem, and it is the only parameter in terms of matter or energy which can be summed for all trophic levels regardless of their length of life-cycle. The total intake of solar energy, λ_0 of Lindeman's nomenclature and our figure, has been called 'primary production' by some, but it is hardly of much biological significance, for, if it were, the most 'productive' biological system would be the 'perfect black body' of the physicist, in which the emission of solar radiation, like its absorption, is at a maximum. The same argument applies to attempts to measure biological activity in terms of rates of flow of individual quanta of energy through the system whilst ignoring the total quantity of energy.

It is not unprofitable to consider the relationships between the 'gross production rate' of Ricker ('corrected productivity' of Lindeman) and the 'activity' which we are considering. The first is an 'annual calorie ration' of potential energy available to the organisms of a given level, regardless of how it is employed or how efficiently exploited. The second is the kinetic energy output of this level, i.e. a proportion of the 'calorie ration' which will depend on the efficiency of exploitation of the animals and which is a measure of the energy removed altogether from the system by these animals. The first is a measurement of the combined stream of energy and matter at a point where they are inextricably mixed, because the matter may circulate many times whilst the energy does not. The 'activity' measures the energy flow only and at points where it is separated from the matter in which it was transported as potential energy.

The practical measurement of this parameter may be tedious, but it is certainly not impossible; limnologists have already evolved methods for assessing the photosynthetic activity of plants, and by measurement of respiration rates of animals, as was done by Bornebusch, the corresponding outflow rates can be measured. In order to compute a total energy expenditure figure for a species over a fixed period, a knowledge of the species' life table would be necessary, and with this should be coupled measurements of respiration rate under environmental conditions for individuals of each age class. Thus an expression representing the integrated energy expenditure of the population of each species would take into consideration the number of individuals in each age class, and the energy expenditure per individual as derived from their measured respiration rates.

As preliminary simplifications it would be necessary, in measuring the first factor, to assume a stable age distribution and consider a fixed time period such as a year whose length would be a multiple of the life periods of the species in the community. As a first approximation to the second factor the use of laboratory respiration measurements would perhaps be permissible, especially for small animals, in view of Zeuthen's (1947) demonstration that respiration rate in such forms is relatively similar in the resting and the fully active organism. The practicability of such a scheme might be first tested on pure laboratory cultures of an animal such as *Tribolium*.

The value of such measurements in assessing the importance of large environmental changes, especially those brought about by human activity, can hardly be doubted.

4. CONCLUSION

It would seem, therefore, that the terms 'productivity' and 'yield' should be retained to signify the rate of intake of food and the quantity accumulated by particular organisms or food groups, but their use should be excluded from the field of energy measurements. For this purpose a new term is required to replace what we have here called 'activity'; it remains for someone with imagination to produce a word which shall be less discordant than 'energy productivity' or 'energy throughput' without at the same time offending the demands of priority and of common sense vocabulary.

5. ACKNOWLEDGEMENTS

This essay is so much the product of other peoples' discussion and thought that it is difficult to trace the origin of most of the ideas expressed. In addition to the authors quoted, and especially W. E. Ricker, whose essay first provoked an interest in the subject, P. H. Leslie, D. H. Cushing, T. T. Macan, A. J. Cain and especially C. S. Elton, while in no way responsible for what is said, have been most patient in discussion and liberal with advice.

REFERENCES

Bornebusch, C. H. (1930). 'The fauna of forest soil.' Forstl. Forsøksv. Danm. 11: 1–224.

Borutzky, E. V. (1939*a*). ['Dynamics of *Chironomus plumosus* in the profundal of Lake Beloie.'] Proc. Kossino Limnol. Sta. 22: 156–95. (In Russian, with English summary, pp. 190–5.)

Borutzky, E. V. (1939*b*). ['Dynamics of the total benthotic biomass in the profundal of Lake Beloie.'] Proc. Kossino Limnol. Sta. 22: 196–218. (In Russian, with English summary, pp. 216–18.)

Clarke, G. L. (1946). 'Dynamics of production in a marine area.' Ecol. Monogr. 16: 321–37.

Harvey, H. W. (1942). 'Production of life in the sea.' Biol. Rev. 17: 221–46.

Hutchinson, G. E. (1942). 'Limnology'. MS. cited by Lindeman, 1942.

Ivlev, V. S. (1945). ['The biological productivity of waters.'] Uspekhi Sovremennoi Biologii, 19: 98–120. (In Russian; MS. translation by W. E. Ricker.)

Lindeman, R. L. (1941). 'Seasonal food-cycle dynamics in a senescent lake.' Amer. Midl. Nat. 26: 636–73.

Lindeman, R. L. (1942). 'The trophic-dynamic aspect of ecology.' Ecology, 23: 399–418.

Lotka, A. J. (1925). 'Elements of physical biology.' Baltimore.

Palmgren, P. (1942). 'Die Populationsgrösse der Vögel als Evolutionsfaktor.' Naturwissenschaften, 30: 217–20.

Ricker, W. E. (1946). 'Production and utilization of fish populations.' Ecol. Monogr. 16: 373–91.

Tansley, A. G. (1929). 'Succession, the concept and its values.' Proc. Int. Congr. Plant Sci., Ithaca, 1926, 1: 677–86.

Thienemann, A. (1931). 'Der Produktionsbegriff in der Biologie.' Arch. Hydrobiol. 22: 616–22.

Windberg, G. G. & Iarovitzina, L. I. (1939). ['Daily changes in the quantity of dissolved oxygen as a method of measuring the primary production.'] Proc. Kossino Limnol. Sta. 22: 128–43. (In Russian, with English summary.)

Zeuthen, E. (1947). 'Body size and metabolic rate in the animal kingdom with special regard to the marine microfauna.' C.R. Lab. Carlsberg, Sér. Chim. 26(3): 17–165.

REVIEWS

NATURE CONSERVATION IN BRITAIN

(1) *Conservation of nature in England and Wales.* Report of the Wild Life Conservation Special Committee (England and Wales). Cmd. 7122. July 1947. 139 pp., 2 folding maps. H.M. Stationery Office, London. Price 4*s*.

(2) *National Parks and the conservation of nature in Scotland.* Report by the Scottish National Parks Committee and the Scottish Wild Life Conservation Committee. Cmd. 7235. 1947. 72 pp. 1 text and 1 folding map. H.M. Stationery Office, Edinburgh. Price 2*s*.

The mills of democratic government grind slowly. It is now all too many years since the idea of national parks was first mooted in Britain, and the nation which prides itself on its love of nature still lags distressingly behind the United States of America, Canada, South Africa, Argentina and many of the countries of Europe, and has no national parks. Nor is its legislation for wild life protection up to date or rationally organized. It is no exaggeration to say that, during the years of gestation of the embryo plans, much that should have contributed to a magnificent realization has been lost, swallowed in the insatiable maw of industrial and urban development. And, although under the aegis of County Planning Committees and of the Ministry of Town and Country Planning an interim stay may be effected of the more obvious vandalism, yet the drain still goes on, much of it through ignorance of natural cause and effect. It would, therefore, be a false economy to shelve these reports on the ground of the necessity for extreme national economy. In fact, the contrary might be argued, that it would be an extravagance we can ill afford not to put the major recommendations into effect with the shortest possible delay. For the rate of retrogression of some elements of our fauna and flora under the pressure of economic developments has been, and remains, quite alarming.

The publication of the 'Dower Report' in 1945 opened a debate, the stage for which had already been set during the war years of 1942 onwards, by the work of a variety of persons and bodies interested in the conservation of the countryside. Much of this activity was canalized through the Council for the Preservation of Rural England, the British Ecological Society and the Nature Reserves Investigation Committee. In 1947 has come the fuller statement of the case in its diversity, in the form of the Report of the National Parks Committee (England and Wales) (Cmd. 7121, July 1947), followed in rapid succession by the two reports under review. Lest, perchance, too much were to be taken for granted, these in their turn were followed in December of the same year by the Prime Minister's report on the 'Needs of the Armed Forces for Land for Training and other Purposes' (Cmd. 7278). This reveals not only another strong competitor for the marginal and extra-marginal land so important to the ecologist, but also a somewhat complacent acceptance of the view that even 'high amenity value' of land comes a long way down in the assessment of its integral use. Indeed, it is open to question whether much of what was hoped for, and its achievement adumbrated in the Chancellor's Land Fund, is not being smuggled out by the back door, wrapped in the Prime Minister's White Paper.

But such misgivings cannot detract from appreciation of the reports before us. Together, and in conjunction with the parent report, on National Parks, they present an integrated scheme for the conservation of the wild life and natural features of the country, for the refreshment of spirit which its quiet and beauty offer, and for the prosecution of a continuing scientific study of its ecology. The former end is to be attained through the establishment of a group of National Parks and Conservation Areas. But the scientific conservation and study of wild life requires something more than the mere allocation of reserve areas, whether these be comparatively extensive, as are the proposed Parks and Conservation Areas, or smaller and carefully selected, as are the National Nature Reserves proposed in the two wild life reports. It requires a planned policy on a national basis, and above all the policy must remain fluid, and modifiable according as new research throws light on the policies and mistakes of the past. Ecologists will therefore welcome warmly the proposal to establish a national Biological Service. They will welcome also the breadth of function to be assigned to it. The total plan envisages a Nature Conservation Board for the whole of Britain, under which will work the Biological Services. The responsibilities can only be summarized here, involving:

(*a*) The scientific and practical management of the National Nature Reserves as centres for the conservation of flora and fauna, and as field laboratories for the staff of the Services and for qualified ecologists in general. And at the same time as providing facilities for students and for amateurs to observe and enjoy natural phenomena.

(*b*) Close liaison with the National Parks Committee, with the free secondment of staff when needed, for aiding the management of not only reserves within National Parks, but also of the whole areas of the Parks and Conservation Areas.

(*c*) The planning and conduct of a continuing programme of research and survey, based on the National Reserves but utilizing freely any land which may be available anywhere and in respect of which inquiry may be profitable.

(*d*) For the realization of a full programme of research into the extremely diverse problems inherent in so diverse a field, the establishment of Terrestrial Research Institutes is recommended. Some of these would be directly financed and maintained under the control of the Biological Service, others it is envisaged will be established by some universities, and the fullest interchange between these and the national service must of course be effected.

(*e*) The representation of informed biological opinion, both centrally and locally on all matters of conservation, protective legislation, pest control, introductions and the like.

(*f*) Maintenance of close liaison, involving where necessary active co-operation, in the form of research programmes, secondment of scientific officers for investigation of specific problems, etc., with other reserve-holding bodies and individuals, with authorities concerned with forestry, agriculture, drainage, water supplies, coastal and other erosion or accretion, and with the Geological Survey, British Museum and like national bodies. The Scottish Report proposes some special arrangements to ensure that the rather different administrative set-up in Scotland may be taken properly into account.

A hint of the complexity of the task the Biological Service may have to face is afforded in the Report of the New Forest Committee (Cmd. 7245, November 1947). Here, in some detail, will be found an attempt to work out for one area, which has already been listed as a prospective Conservation Area and Scientific Area, a means whereby it may be conserved for popular enjoyment and for scientific study, while at the same time safeguarding the needs of those who live there and derive their livelihood from it. There are special features of the New Forest, some of which will not be inherent in other regions. The Report, however, conveys a minutely analysed picture of the interlocking, and sometimes conflict, of interests which will have to be faced in determining a plan for land usage anywhere in Britain. It is particularly significant that the Committee, of which no ecologist was a member, have approached the problem of the conservation of the Forest's wild life with commendable caution. They conclude, 'The difficulties are greater because those in charge cannot be expected to have a detailed knowledge of the species in need of protection', and recommend strongly that a qualified curator be appointed 'with charge of all fauna and flora within the area'. Many ecologists will agree in expressing the opinion that the Biological Service is the body to which such a curacy should be offered.

It is a vast field, with infinite room for successes and failures, and much will depend on finding the right starting-points and above all on finding the right personnel for the Service. This latter will be by no means easy. Ecology, particularly animal ecology, has for so long been a Cinderella among the biological sciences in this country that only a very small proportion of British biologists may be regarded as competent even to begin an investigation of where and how to start. There need be little fear as to whether the men and women will come forward for training, as the Service becomes established. There is plenty of interest in field problems among young biologists, and only economic pressure now diverts the best of these into other work.

Readers interested in the details of the finance and administrative organization involved in the proposals must be referred to the reports themselves. Suffice it here to draw attention to the fact that the apparent low cost of acquisition of reserves and of the Biological Service itself must be looked at in the light of the dependence of the plans on the proposals already made by the National Parks Committee. The one is so closely dependent on the other that, as the Wild Life Conservation Committee indicates, in the absence of any provision for Nationa Parks and Conservation Areas the demands for natur reservations would inevitably be vastly greater. Even so the total estimated capital costs of the whole will lie wel within the £50,000,000 of the Land Fund. It cannot however, be emphasized too strongly that this is not to b regarded as a capital charge to the country, but as a capita investment, the returns on which in terms of huma happiness and knowledge, as also of actual increase o economic wealth and efficiency, will be at a high rate o interest.

L. A. HARVE

POPULATION INSTABILITY

A. D. Voûte (1946). *Regulation of the density of th insect-populations in virgin-forests and cultivate woods.* Archives Néerlandaises de Zoologie, 7 435–70.

The main thesis of this paper is that insect populations i cultivated woods commonly show violent fluctuations i abundance, leading to periods of severe damage, wherea in virgin forests and mixed woodlands the population remain much more stable, and but rarely reach such hig values as to cause serious defoliation. Examples to prov this are taken from a wide range of the continental literatur on forest entomology, much of which is unfamiliar t British ecologists.

For the many different sorts of factors which affec populations, Voûte, although he writes in English, choose terms different from those in general use in this country and some of them tend to give the wrong impression. Fo instance, 'selective factors' have no direct relation t natural selection, but are those factors which damage o destroy one individual rather than another, as might hailstone, or a predator. 'General factors' are those whic have a physiological effect on all individuals, such a climate and food. Voûte correctly recognizes the funda mental importance of density–dependent factors, whic he simply calls 'dependent factors', and rejects the ide of Bodenheimer that climate can have a regulating in fluence on animal populations. He also makes the vali distinction between simple density-dependent factors, an specific parasites and predators which he calls 'modifiabl factors'. Once a reader has become used to the strang terminology he can begin to understand the underlyin ideas.

Like many economic entomologists, Voûte confuse his theoretical discussion of population oscillations b defining population densities in terms of the populatio density below which no economic damage occurs. Fo him, densities below this level are the 'natural density'— a most unfortunate term. If a population increases abov this, then 'independent satiate factors' (i.e. general pre dators such as birds, which do not increase in response t pest abundance, and which eat the same number, bu a smaller proportion, of the pests when the pest is speciall abundant) have a smaller restraining effect on the increas of the pest, which thereby reaches the 'escape phase' an increases more rapidly than ever. Eventually, hig population densities are reached, and 'modifiable factors such as monophagous insect parasites become increasingl effective, and cause a 'crisis' in which the populatio density rapidly falls once more to the 'natural density'.

During the period of the 'natural density' the pest is, according to Voûte, in labile equilibrium with its surroundings. In the escape phase and the crisis of a 'gradation' (i.e. increase to outbreak scale) the situation is believed to be due to the relaxation of the effects of the general predators, and the increase in the effectiveness of the monophagous parasites respectively. For these three phases, then, Voûte considers that three entirely different explanations are needed. Although he refers to A. J. Nicholson's paper on 'the balance of animal populations' (this *Journal*, 1933, 2:131–78) he clearly misses the significance of Nicholson's conclusion that large and increasing oscillations in population density should occur if an insect is attacked by a monophagous parasite. And although Voûte shows clearly that in some instances at least the 'crisis' is due to a monophagous parasite, he does not see that it may be the effect of the host's crisis on the parasite which causes it to be rare or absent in the periods of the natural density and the escape phase, and that the temporary rarity of the parasite may allow the host to increase in the escape phase.

Another problem of great interest to present-day ecologists is the reason for the relative stability of the population densities of insects in mixed woodlands and primeval forests as compared to the violent oscillations in the insect populations in pure stands of cultivated woods. Voûte points out that the fauna of a mixed wood is much richer than that of a pure stand, and contains a higher proportion of general predators, and a lower proportion of monophagous parasites than a pure stand. In woods with a great mixture of forest trees, as in tropical rain-forest, ichneumon flies and their allies are rare. Voûte believes, with Nicholson, that general predators, having the ability to feed on a range of species, and choosing whatever species is abundant at the time, may be agents promoting stability. Where a specific parasite or specific predator attack a pest, then conditions are closer to those considered mathematically by Nicholson and Bailey, who predicted population oscillations of increasing amplitude. It appears to the reviewer that it is no coincidence that the classic cases of violent oscillations in animal populations are the insects of the German spruce forests (studied by Schwerdtfeger and others at Eberswalde), and the mammals of the tundra and the Northern forests.

Voûte is a strong advocate of the planting of mixed woodlands, by which simple means he believes—on very good evidence—that the insect damage in commercial forests can be minimized, and the woodlands made more productive of timber.

G. M. VARLEY

SPECIES FORMATION ON ISLANDS

D. Lack (1947). *Darwin's finches.* x + 208 pp. 8 plates and 27 text-figures. Cambridge University Press, Bentley House, 200 Euston Road, London, N.W. 1. Price £1. 1*s*.

Probably no book is of such perennial interest to the naturalist as Darwin's *Journal of the Voyage of the Beagle*, and in that work no part is more enthralling than Chapter XVII which deals with the Galapagos Archipelago. The fauna and flora of the different islands show resemblances and differences, both amongst themselves and when compared to their nearest allies in South America, of a type which played a big part in convincing Darwin of the truth of the theory of evolution and in indicating some of the causal factors involved. An important element in the fauna is the Geospizinae, a subfamily of finches endemic to the Archipelago except for an outlying genus on Cocos Island, 600 miles to the north-east.

The group, called in the work here reviewed, 'Darwin's finches' exhibits all the main peculiarities of Galapagos biology, subspeciation, adaptive radiation and some apparently non-adaptive evolution. They are now very well known taxonomically and Mr Lack, by visiting the principal British and American museums, was able to study well over three thousand specimens of the fourteen species which he recognizes. Moreover, in the four months which his expedition spent on the islands they were able to make essential field observations without which the interpretation of the museum data would be very incomplete, and to establish some of the species alive in a Californian aviary where their failure to interbreed was confirmed. With these advantages, and after a great deal of hard work, Mr Lack has brought together an account of island speciation in a limited group of organisms exceeded in bulk, perhaps, only by Crampton's monumental study of *Partula* in the Society Islands, but far exceeding that work in its interest for the general biologist. I may say that even an entomologist found every chapter of absorbing interest, not least because of the topics for debate which are continually brought forward. An attempt has been made to divide the work into Part 1 (Chapters 1–11) 'Description', and Part 2 (Chapters 12–16) 'Interpretation', but in fact of course there is almost as much interpretation in Part 1 as in Part 2; in the classification adopted, for instance, and in the discussion of the beaks and colours of the birds. It is impossible to collect or arrange scientific data without some theory which automatically introduces an element of interpretation.

The most important new conclusions may be singled out. It is shown, in a number of examples, that species originally defined by ordinary taxonomic methods do not interbreed. To feel that the general classification of the group is on the right lines greatly simplifies arguments about its evolution. It was shown by experiment in several species that the beaks of these birds serve as the recognition marks which help to prevent cross-pairings. This type of recognition is apparently unusual in birds, especially in the Fringillidae which more often differ markedly in colour. However, the author supposes that the beaks were primarily evolved in relation to feeding habits and were only secondarily used for recognition. The treatment of subspeciation, individual variation and general variability, if not on entirely new lines, is very thorough, employs the latest statistical methods, and is related to such topics as size of population, degree of isolation and range of habitats occupied. Probably the most original contribution and certainly one likely to have a wide application elsewhere is the study of the effect on a group of allied species of the absence in certain places of one member. Thus *Geospiza conirostris* on Hood Island spreads into the habitat occupied on some of the other islands by *G. magnirostris*. It shows that whenever this type of spread into a new habitat occurs the local race of the bird is modified in the direction of the species it has

replaced. It is argued that when all the species are present they are confined by competition to narrower habitats and their beaks, etc., become specialized for a less varied food supply. It seems that we have here a powerful method for the general study of natural variation and adaptation. There are many areas where some of a group of allied species are absent and a great deal could be done in studying the effects on those that remain. Finally, there is valuable discussion of the character of the faunas of oceanic islands in general and of their method of evolution.

Mr Lack is firmly convinced of the paramount importance of natural selection in the evolution of species and of the particular formulation of the theory 'that two species which live in the same habitat must differ in their ecology or one will drive the other out'. Ecology in this sense is almost synonymous with food habits and it becomes necessary to show, where allied species share one territory, either that they live in different divisions of the habitat or that their feeding habits are different. Unfortunately quantitative information as to the food of the Geospizinae, as indeed of all birds, is lamentably deficient and there seems to be a certain amount of circular argument from beak to food habits and back again.

It is admitted on page 136 that competition for food will only force species to live in separate habitats when food is a limiting factor for abundance. No evidence is presented that this is so in birds; it clearly is not the limiting factor for most insects in most years and for most plant-eating insects the difficulty is rather to explain why they are not more abundant. Surely the whole argument is a great simplification of extremely complex facts? It depends on simple clear-cut competition in one aspect only of an animal's life. In practice, with varying local conditions, fluctuating climate and food supply, different species will alternately have some advantage, and there seems no reason why a number should not co-exist in unstable equilibrium at a population level well below the maximum possible.

A speculative phylogeny for the Geospizinae is provided in Chapter 11. I have the impression that a good deal of it could as well be read backwards as forwards. In the absence of fossil evidence, or of some other really reliable evidence as to the main direction of evolution, the tracing of phylogenetics at this level of divergence is scarcely possible.

Mr Lack has intentionally interlarded a big body of facts with a spice of theory and I think he has judged the mixture very well. It is in any case much more difficult than is sometimes supposed to provide 'pure fact'. But the test of theory is not only its truth (in biology that usually lies somewhere far over the horizon) but how far it suggests new unthought-of experiments. On this test Mr Lack's theories come out reasonably well, but there seems to be a permanent dichotomy between those who find their zest in the natural selection theory and those who cannot. The problem, for instance, of whether certain specific characters (e.g. beaks of Geospizinae) are or are not adaptive (vague term) is one involving studies of field populations, genetics, and variation. It is a problem which might be largely solved by teams of workers dealing for a number of years with a particularly favourable example. It is not one, I think, which can be settled in a four months' stay, even if supplemented by the examinations of skins in museums. It is not, of course, that the beaks may not be adapted to different uses, but that it is extremely difficult to prove that this is so to an extent which affects the level of the population.

Such, however, are the virtues of *Darwin's finches* that one could argue with the author for a good many more pages. The desire to do so is the best recommendation of the book.

O. W. RICHARDS

THE COMMUNITIES OF SEA WRACK AND HOT SPRINGS

H. O. Backlund (1945). *Wräck fauna of Sweden and Finland: ecology and chorology.* Opuscula Entomologica, Suppl. 236 pp. 23 text-figures, photos and maps; 17 plate-photos. Lund.

S. L. Tuxen (1944). *The hot springs of Iceland, their animal communities and their zoo-geographical significance.* The Zoology of Iceland, 1 (Pt. 2): 1–205. 53 maps and text-figures, and 13 photos. Copenhagen and Reykjavik. Price Kr. 15 for this part.

These two papers are examples of the best modern work on 'scientific natural history'. They are valuable preliminary surveys of unusual habitats which describe not only the fauna but also the flora and environmental factors: both authors express disapproval of a current tendency to apply mathematical techniques in such work and, by their example, certainly provide sound arguments for the value of a 'natural history' approach.

An environment which is extremely rich in plant material, but is liable to be completely dispersed by the next storm; which, by the heat generated within, causes overlying snow to melt when the temperature of nearby areas is below freezing-point, and in which biological activity is so intense that very large populations of a wide range of animals are developed despite the essentially ephemeral character of the substrate: such are the outstanding features of the peculiar habitat studied by Backlund.

The study might be classed as a comprehensive preliminary survey: it provides a detailed picture of the types of animals to be found in the beds of decomposing *Fucus* and *Zostera*, which are a conspicuous feature on the Baltic shores and of the environmental factors which govern their existence. Because of its comprehensive nature no attempt is made to assess absolute numbers of animals, although approximate relative figures are obtained by the use of the Tullgren funnel in most groups; flying forms were simply captured with a hand net, whilst some groups such as mites are completely ignored. While the introduction contains a criticism of the tendency toward the use of the quantitative method in ecology as an aim in itself, on the grounds that our present inexact methods and lack of knowledge of growth rates and life histories make such studies fruitless, the mode of attack on factors controlling distribution is the alternative one of comparing the findings of laboratory experiments on preferenda and tolerance ranges with the results of field studies and combining with this careful 'straight natural history' work on biology and feeding habits. The excellent section on this subject contains much valuable basic material.

Backlund's paper arrives at a number of general conclusions of greatest interest to the ecologist: he shows that there are diurnal vertical migrations of many species in the wrack, following a cycle of reduction and restoration of water content in the upper layers, that the constant high temperature in the wrack greatly reduces seasonal variations in growth rate and reproductive activity in many species, and that the members of the wrack fauna can all survive immersion in sea water, while many of them can regain the land when washed out to sea for a short distance.

His conclusions with regard to the control of population size by biotic factors are interesting. He believes, as a result of his feeding studies, that population size is limited by competition for food in many cases where superficial examination would lead one to the reverse conclusion. This is because the herbivorous and saprophagous forms tend to be highly specialized in their exact food requirements, so that the actual food available to a species is very much less than the potential food supply. In certain Dipteran populations he concludes that these are never limited by their parasites in practice, because the life span of a single wrack community is not long enough for the parasite population to catch up with that of the host. In other words, the abiotic factor replaces the biotic in controlling the population size: this presumably means that the abiotic or catastrophic factor is itself density-dependent, for otherwise (as pointed out by H. S. Smith, 1935, J. Econ. Ent. 28: 873) the population size would presumably not be controlled at all. It is rather difficult to visualize the nature of such a density-dependent factor in this case, but the matter could be made the subject of experiment.

That Backlund is not entirely averse to the use of statistical methods in ecological studies is evident from his use, to summarize the 'sociological structure' of the wrack fauna, of the methods employed by Kulczynski (1927, Bull. Int. Acad. Cracovie, Suppl. 2: 57–204) and since extended to the analysis of the sociological relations of species within a community by Agrell (1945 Förh. Kungl. Fysiogr. Sällsk. 56 (9): 1–15). By the use of this method he concludes that there is no marked tendency for correlation between the distribution of the different species, and hence, presumably no significant degree of dynamic interdependence. If one accepts dynamic interdependence between constituent species as the criterion of the existence of a 'Biocenose'—as does Däniker (1939, Ber. Schweiz Bot. Ges. 49: 522–40) 'Die Biocenose ist eine Lebensgemeinschaft von Pflanzen und Tieren, deren Individuen durch zahlreiche ökologische Korrelationen miteinander und mit ihrem Standort verbunden sind...' —one can only conclude that the wrack fauna does not constitute such a community. Backlund considers this point, but concludes that 'the populations of wrack beds should be considered as belonging to a distinct community, because the large number of eucocoenic animals (stenotopic or animals restricted to the biotope) as well as the high abundance are caused by the specific ecological conditions of the biotope'.

It seems to me that this dilemma, which is only avoided by inconsistency, is surely due to the use of a wrong method. Backlund is concerned to show whether or not the wrack fauna is a distinct community from other shore communities. He should, therefore, have applied Kulczinski's original method—and not Agrell's modification which is designed to investigate grouping *within* habitats ('biotopes')—to all shore animals, including the wrack forms among them. When thus compared with other shore forms the degree of association of the wrack forms would have been evident.

Tuxen's paper covers perhaps an even wider range of related subjects, including the chemistry and physics, geology and geography of the hot springs; taxonomy, morphology, physiology and life histories of their organisms and those of the nearby soil; their geographical distribution; and their relation to Ice Age faunas. Careful field measurements are correlated with the distribution of the animals and with experiments on their physiology. Calculations of the annual variation of received sunlight energy are made to account for the probable two months' resting stage in the winter. 'Tullgren' methods are used for obtaining relative numbers for the soil fauna and it is argued that these should be related to area of soil sampled, and not to volume—in opposition, e.g. to Agrell (1941, Opusc. Entom. Suppl. 3: 1–236).

The paper contains a vigorous polemic against the 'cult of figures' in ecology and in support of the hypothesis that animal communities possess properties which cannot be elucidated solely in terms of their constituent organisms—in opposition to Bodenheimer (1938, 'Problems of animal ecology'). This argument is really concerned with two separate lines of work. First, there is Bodenheimer's contention that the community concept is a barren and inexact one and that 'coactions' and competition are of no significance in the integration of the living community. These views now receive little support except from the school of Uvarov and, since they are adequately answered by H. S. Smith (loc. cit.) will not be further discussed here. Secondly, it concerns the efforts of Agrell and others to develop the statistical approach to community studies which was initiated in the field of botanical ecology by the school of Braun Blanquet. Tuxen justly criticizes Agrell for basing his 'objective' community distinctions on 'subjective' sampling localities based on the macro-vegetation types; but this is no criticism of the basic ideas behind the method, which is undoubtedly capable of giving reliable information not evident simply from unaided field studies.

The two papers both bring into prominence the current division of opinion between the 'back to Fabre' outlook which demands more careful field observation and less wholesale application of standardized and uncritically applied numerical techniques regardless of the autecology of the species concerned; and the alternative attempts to utilize the quantitative precision of statistical techniques in order to arrive at more than purely qualitative and subjective conclusions about the structure of communities. It is not difficult to find examples of the misapplication of both types of method, but quite evidently both are necessary, each in its own field, as is demonstrated by Backlund's paper. If one is concerned with simply correlating relative abundance with environmental factors a purely relative technique suffices; whereas if, like Bornebusch, one is concerned to assess the relative importance of different species in the turnover of organic matter in the soil, absolute biomass figures as well as a measure of rate of activity must be obtained. Careful field studies combined

with physiological experiment will lead directly to an idea of the niche of the individual species. But the study of the impact of environmental factors on population size and the 'vertical' and 'horizontal' interaction of species demands a quantitative approach. The type of study which is definitely to be discouraged is that which falls between the two stools and while not attempting to elucidate population structure, applies some inflexible numerical method regardless of the autecology of the species concerned.

A. MACFADYEN

SHORT REVIEWS

The Indian Ecologist. Vol. 1, no. 1, pp. 1–66 (April 1946) and no. 2, pp. 1–48 (January 1947). Edited for the Indian Ecological Society by F. R. Bharucha, Department of Botany, Royal Institute of Science, Bombay. Price per volume, 15 rupees.

Attention was drawn in the *Journal of Animal Ecology* (1943, 12: 60) to the formation of the Indian Ecological Society in 1941. It is satisfactory that the Society has now been able to launch, on a modest scale, a general journal for Indian plant and animal ecological studies. The first two numbers contain papers on microclimates of vegetation, contour strip-cropping, communities of low-lying lands that get very wet in the rainy season, drought resistance in sugar cane, the histology of a plant with floating roots (*Sesbania*), a taxonomic key to Compositae of Bombay, and a good deal of discussion and records dealing with the Society's organization. The one paper on animal ecology deals rather unexpectedly with the habits and adaptations of adult Trichoptera near Newcastle-upon Tyne. The format is almost exactly like that of the *Journal of Ecology*, indeed the outer resemblance suggests an analogy with 'Mullerian mimicry' in insects, since ecologists will be enabled to recognize the common pattern at a distance. It is to be hoped that *The Indian Ecologist* will be able, as material begins to accrue and the Indian Society grows in influence, also to develop a high quality of contribution, with the advantage of special experience with tropical communities of plants and animals. One small point may be raised: it is inconvenient to have the paging start afresh with each number within a volume: could they be made continuous for each whole volume?

C.E.

Conseil International pour l'Exploration de la Mer. *Enquiry into the problem of climatic and ecological changes in Northern waters, etc.*

We have received a very interesting circular announcing the desire of this organization to collect materials concerning fluctuations in ecological conditions and numbers of marine populations in northern waters, as well as those of any terrestrial ecosystems or populations that may show associated changes. The very marked amelioration of conditions and the northward movements of some populations or whole communities in recent years has been especially noticed in the marine fisheries and current systems, above all in the development of the northern cod fisheries; also in northward shifts of Baltic bird life and onset of mild climatic conditions in Northern Labrador, with apparent effects also upon the seasonal movements of caribou. The present enquiry apparently has no limits to its scope, so long as any chance of correlating these changes with one another can usefully be explored. There is already a good deal of historical evidence that the changes are recurrent, so that the longer trends are complicated by shorter swings, as with the northward shifts of species in 1820–30, 1840–50, 1870–80, and 1920 onwards, mentioned in the circular. Ecologists are asked to communicate any information they may think relevant and useful, to Dr Å. Vedel Tåning, Charlottenlund Slot, Charlottenlund, Denmark, preferably in December of each year (for any one annual report). Any references, reprints, or other information, will be kept on file by the Conseil, after being used. C.E.

Edmund Sandars (1946). *An insect book for the pocket.* 349 pp. ($4\frac{1}{4} \times 5\frac{3}{4}$ in.), 36 pp. of coloured plates, numerous text-figures. Oxford University Press, Amen House, London, E.C. 4. Price 10*s*. 6*d*.

Until this book was published there was no small book on British insects that gave both convenient and reliable information about the different kinds of British insects that the naturalist is likely to be interested in. None can either know or explain to others the characters of all our 20,000 insect species; but the author decided on a simple rule of thumb that has enabled him to overcome the difficulty of choosing what species to describe, by omitting all those less than about half an inch long, which leaves him with about 130 families. He does, however, mention all the orders, and in addition, the arachnids, myriapods and woodlice. There are pleasing and fairly accurate coloured pictures of representative types, and the text expands this treatment under the various taxonomic groups. Naturally, this is no guide to species, only to some of the main types of form and habit; but the number of species that there are in each group is always mentioned, and how many of them are 'large' in the sense the author uses. Readers of the earlier books on birds and mammals by Mr Sandars will recognize and enjoy his extraordinarily crisp, accurate and sometimes amusing style. His death in 1942 removed one of our most talented abstracters of scientific material, whose integrity in conveying knowledge to the public was of a high standard. The present book has been edited by Dr B. M. Hobby, which is a further guarantee of its accuracy, and completeness as far as is possible in such a small compass. Many ecologists who are not trained entomologists will enjoy having this book, and find it invaluable as an avenue to deeper acquaintance with insect ecology. C.E.

A. D. Imms (1947). *Insect natural history.* xviii + 317 pp., 40 coloured plates (106 photos), 32 black and white plates (104 photos), 40 text-figures and 8 distribution maps. The New Naturalist series. Collins, 14 St James's Place, London, S.W. 1. Price 16*s*.

Most of the 'wild life' of this country consists of insects; nevertheless, we have had few general books on their natural history that meet modern standards and needs. Dr Imms, whose general academic text-books on insect morphology and biology are well known and in daily use by entomologists, has now given us a really first-rate book,

almost a series of essays, on many of the interesting aspects of field entomology. After some general introductory chapters on structure and classification, he treats successively food habits, biological control, gall formation, protective devices, breeding methods, water insects, and social life at different levels of aggregation. The book does not by any means depend only upon its numerous coloured plates to attract the reader, although these, especially the ones by Mr Beaufoy, are of higher technical standard than usual, as well as being often beautifully chosen. By the use sometimes of anaesthetics or chilling, the photographers have obtained groupings of unusual interest. The text itself, is extremely lucid and interestingly written, and shows a power of selection from the abundant entomological literature that will especially appeal to ecologists. It seems (from notes given in a review of this book in the Ent. Mon. Mag. 1947, 83: xlvii) that there are a certain number of detailed mistakes in naming the insects. But the book can be strongly recommended both for general reading, and for reference on a number of subjects which cannot easily be learned about without a wide search of literature. C.E.

R. C. McLean & W. R. Ivimey Cook (1946). *Practical field ecology: a guide for the botany departments of universities, colleges and schools.* 207 pp. ($4\frac{3}{4} \times 7\frac{1}{4}$ in.), 50 text-figures and photos, 1 coloured ecological map. George Allen and Unwin Ltd., 40 Museum Street, London, W.C. 1. Price 9*s*.

A book giving in convenient compass all the practical methods that might ordinarily be required in a botanical field survey cannot fail to be useful to teachers and research workers, and animal ecologists will be glad to have this new technical reference book. Its main subject is the measurement and mapping of the terrestrial plant association or complex, and the climatic and soil environment, but there are also chapters upon ponds and streams, on the seashore, and on herbarium methods adapted for ecological survey material. The treatment is succinct but thorough. It cannot be denied that one feels a certain over-stressing of the rigid practical method, the exactly planned tool box, and the glory of fact finding by team-work; but perhaps the authors themselves would agree with Thoreau when he said: 'I do not mean to prescribe rules to strong and valiant natures, who will mind their own affairs whether in heaven or hell, and perchance build more magnificently....' No doubt any good teacher will know how to point the conclusions and ideas that emerge from such detailed surveys, but this book hardly alludes to them: it is an excellent means to an end whose description must be sought in other publications. Three useful appendices contain keys to grasses by means of vegetative characters, to the chief genera of British seaweeds, and to the higher fungi. C.E.

Alastair N. Worden (editor) (1947). *The U.F.A.W. handbook on the care and management of laboratory animals: with an Appendix on statistical analysis.* xvi + 368 pp., 70 text-figures and photos. Baillière, Tindall and Cox, 7 and 8 Henrietta St, Covent Garden, London, W. C. 2. Price 31*s*. 6*d*.

Ecological studies often require extensive laboratory experiments on populations that have been bred from wild stock and can be kept under controlled conditions, sometimes also upon the standard tame laboratory animals. The phenomenal amount of good information about methods of management condensed into this book (published on behalf of the Universities Federation for Animal Welfare, who are a sensible humane organization that does not attempt to fight vivisection as such), was made possible by the co-operation of a number of authors who have contributed separate chapters. The laboratory animals, or species that have now been turned partly into regular laboratory animals, include the rabbit, guinea-pig, brown rat, black rat, house-mouse, 'wild' house-mouse, wood mouse (*Apodemus sylvaticus*), deer mouse (*Peromyscus*), cotton rat (*Sigmodon*), vole (*Microtus*), golden hamster (*Mesocricetus auratus*), ferret, hedgehog, pigeon, and canary, all of which are considered in some detail as regards cages, food, breeding, diseases, etc. There are chapters on legal aspects, on the animal laboratory in general, on pests of animal houses, and notes on certain frogs, fish, and some other animals. The statistical appendix by C. W. Hume aims at presenting the subject in a form that can be assimilated by the less highly mathematical biologist. Its concluding sentence perhaps sums up the outlook of the society that organized the handbook: 'The writer will not have burned his midnight oil in vain if as a result even one rat fewer shall be required in some experiment involving discomfort.' The editor, Prof. Worden, should be proud of having produced such an obviously authoritative work, and persuaded such a large number of people to meet on a common ground of humanity and utility. C.E.

ERRATA

This *Journal*, 1947, vol. 16, p. 94. Review of papers by Ivar Agrell:

For (1941) read (1945).
For (1944) read (1941).

NOTICES OF PUBLICATIONS ON THE ANIMAL ECOLOGY OF THE BRITISH ISLES

This series of notices covers most of the significant work dealing with the ecology of the British fauna published in British journals and reports. Readers can aid the work greatly by pointing out omissions and sending reprints of papers and reports to the Editor, *Journal of Animal Ecology*, Bureau of Animal Population, Department of Zoological Field Studies, 91 Banbury Road, Oxford.

Duplicate copies of these notices can be obtained separately in stiff covers (printed on one side of the page to allow them to be cut out for pasting on index cards) from the Cambridge University Press, Bentley House, 200 Euston Road, N.W. 1, or through a bookseller, price 3*s*. 6*d*. per annum post free (in two sets, May and November). Back numbers are available at half price.

Selection and abstracting has been done voluntarily by H. F. Barnes, A. C. Evans, R. S. Fitter, E. M. O. Laurie, C. Matheson, E. Nelmes, W. S. Richards, M. R. Shorten and H. N. Southern; checking by B. M. Hobby.

Within each section the groups are arranged in alphabetical order. Papers dealing with technical methods are dealt with in the appropriate sections.

CONTENTS

	PAGE
1. Ecological surveys and the relations of animals to habitat conditions	88
(*a*) Marine and brackish	88
(*b*) Fresh water	89
(*c*) Land	90
(*d*) Small islands	93
2. General reports and taxonomic studies of use to ecologists	93
3. Parasites	94
4. Food and food habits	95
5. Population studies	96
6. Migration, dispersal and introductions	99
7. Reports of organizations	100

1. ECOLOGICAL SURVEYS AND THE RELATIONS OF ANIMALS TO HABITAT CONDITIONS

(*a*) Marine and brackish

Brown, E. S. (1947). '*Psammathiomyia pectinata* Deby (Chironomidae) and other Nematocerous Diptera in Cornwall in 1946.' Ent. Mon. Mag. 83: 81–2.

This is an apterous chironomid which occurs near low tide level. As they drown in sea water, the imagines must either shelter over high tide in rock crevices, or their lives must be bounded by two successive high tides. Records and habitat of 21 species of Nematocera are also given.

Evans, R. G. (1947). 'The intertidal ecology of Cardigan Bay.' J. Ecol. 34: 273–309.

Climatic and tidal factors in the Bay are described, and tidal levels and exposure to air. The distribution of the following species was studied with reference to local variation in environmental conditions, mainly those of exposure to wave action, rock configuration, and relationship to other organisms: Crustacea: *Balanus balanoides*, *Chthamalus stellatus*. Polychaeta: *Sabellaria alveolata*. Mollusca: *Gibbula cineraria*, *G. umbilicalis*, *Littorina littoralis*, *L. littorea*, *L. neritoides*, *L. rudis*, *Mytilus edulis*, *Nucella lapillus*, *Osilinus lineatus*, *Patella athletica*, *P. depressa*, *P. vulgata*.

Fowell, R. R. (1945). 'The ecology of a rock pool.' Proc. Swansea Sci. and Field Nat. Soc. Vol. 2, pts. 6 and 7: 192–212.

Fauna and flora of a pool at Langland Bay, Gower. Lists of Protozoa, Porifera, Coelenterata, Annelida, Crustacea, Mollusca, Polyzoa, etc.—about 90 species in all. Lists of species associated with the empty tubes of *Lanice conchilega* and with the seaweed *Corallina officinalis*. Most of the animals are new records for Glamorgan.

Lucas, C. E. & Rae, K. M. (1946). 'The plankton of the North Sea in relation to its environment. Part I. The hydrological background in the southern North Sea, 1930–37.' Hull Bull. Mar. Ecol. 3, No. 17: 1–33.

There was a cycle in salinity reaching a peak in the winter 1934–5 and followed by an equally marked decrease.

Walker, T. G. (1946). 'Terns in Anglesey.' Trans. Anglesey Antiq. Soc. and Field Club, 1945: 64–6.

Anglesey is the only Welsh county frequented regularly by common, arctic, little, sandwich and roseate tern. Sandwich terns arrive first, roseate and little terns last, reaching Llanddwyn at the end of May. Notes on nesting, food and Welsh names.

Went, A. E. J. (1946). 'Irish fishing weirs—1. Notes on some ancient examples fished in tidal waters.' J. R. Soc. Antiquaries Ireland, 76: 176–94.

Historical and descriptive information about 11 fishing weirs mainly in south and south-east tidal waters.

Went, A. E. J. (1946). 'Pilchards in the South of Ireland.' J. Cork Hist. Archaeol. Soc. 51: 137–57.

Describes methods of fishing, curing and localities where cured in the past.

(*b*) Fresh water

Browne, F. Balfour- (1947). 'The British species of *Noterus* (Col., Dytiscidae) and the problem of changing range of species in Britain.' Ent. Mon. Mag. 83: 24–8.

Discusses the distribution and synonymy of *N. clavicornis* and *capricornis*. The former occurs mainly in England south of the border counties and in Ireland, but has been recorded from the Isle of Reasay and from a pool which has existed only for the last 18 years, in Dumfriesshire. *N. clavicornis* has a similar discontinuous distribution, but is also absent from S.W. England and S.W. Ireland. The wide range of these species on the Continent renders interpretation of this discontinuous distribution in terms of a southern withdrawal unlikely. The occurrence of *capricornis* in a new pool in Dumfriesshire suggests rather a northward extension of range.

Browne, J. Balfour- (1947). 'On the aquatic Coleoptera of Pembrokeshire.' Ent. Mon. Mag. 83: 18–19.

Ninety species listed. *Ochthebius poweri* (Hydrophilidae) is restricted to damp vertical cliff just above high-tide mark, and is only recorded elsewhere in Britain from South Devon and Dorset. *Hydrovatus clypealis* (Dytiscidae) is another Lusitanean form.

Ewer, R. F. (1947). 'The behaviour of *Hydra* in response to gravity.' Proc. Zool. Soc. Lond. 117: 207–18.

Buds up to three days of age migrate upwards, and this response is shown to be to gravity and not to oxygen concentration. It is presumed that this behaviour aids in dispersal.

Lacey, W. S. (1946). 'Notes on the orb-cockle, *Sphaerium corneum*, L., and its behaviour in toxic solutions.' Northw. Nat. 21: 188–97.

S. corneum was found in 1944 to be establishing itself in a settling tank of approximately 200,000 gal. capacity belonging to a bleach works in Bolton, and had become so abundant that living and dead individuals frequently became caught in the cloth and contaminated it. The tank was supplied with water from the River Croal, which first passed through three sand filters, and both river and filters were found to contain the mollusc. Specimens from the tank were identified as *S. corneum* living under crowded and unfavourable conditions. Since the water was purified by the feeding of the molluscs, they were not destroyed, but the outlet pipe was fitted with a filter of about $\frac{3}{16}$ in. mesh and arranged to project a few feet into the water and away from the sides and bottom of the tank, where the molluscs were most numerous. The use of toxic substances in control was undesirable, but their effect on *S. corneum* was investigated in the laboratory. It proved very resistant; dilute solutions of copper sulphate were extremely toxic, though the animals lived fairly normally for six days before dying. Sodium arsenite was markedly more toxic than sodium arsenate.

Pearsall, W. H. (1947). 'Water supply and biology.' Nature, Lond. 160: 176–8.

Biological methods have largely replaced the chemical ones formerly used for determining the character of water supplies. Many of the biological problems of water supply centre round the control of impounding reservoirs, which offer a habitat for plants and animals to live in. The problems presented by algal growth and the need to exploit the reserves of nitrogen and phosphorus, where fertile surface waters are used for water-supply purposes, are discussed.

Vane, F. R. (1946). 'Longevity of mayflies.' Northw. Nat. 21: 252–3.

Survival periods of one and four weeks are recorded for two adults of *Cloëon dipterum* reared in captivity and their longevity is attributed to conservation of the energy normally expended in flying and mating. Records by other investigators of mayflies surviving for two to three weeks are given; one finds a direct correlation between the duration of the subimaginal and imaginal stages.

(c) Land

Allen, A. A. (1947). '*Brachinus crepitans* L. (Col., Carabidae) away from chalk.' Ent. Mon. Mag. 83: 80.

Records from the Thames estuary and West Sussex.

Allen, E. E. & Rutter, J. G. (1945). 'A survey of the Gower caves with an account of recent excavations. Part I.' Proc. Swansea Sci. and Field Nat. Soc. Vol. 2, pts. 6 and 7: 221–46.

An account of 15 of the Gower Peninsula caves, with bibliography and list of the fossil species recorded from each. Three species—*Talpa* sp., *Neomys* sp. and *Microtus* sp.—recorded from Gower caves for the first time; also half of lower jaw, with two milk teeth, of *Elephas antiquus*, from Bacon Hole.

Andrewes, C. H. (1947). 'Hemiptera-Heteroptera in Merionethshire.' Ent. Mon. Mag. 83: 95.

Twenty-five new county records. *Anthocoris sarothamni* is new to Wales.

Arthur, D. R. (1947). 'Observations on *Metopolophium festucae* Theob. (Hem., Aphididae) in South Wales.' Ent. Mon. Mag. 83: 48–51.

In Glamorgan and Monmouth during 1942–4, russet patches appeared among winter oats due to shrivelling of the leaves through heavy attack by *M. festucae*. Spring-sown crops were only slightly affected. Damage first appeared as dark red markings round the chlorotic area marking the site of stylet penetration. These markings enlarged until the whole leaf turned pale yellow and shrivelled. Potash and phosphate deficiencies did not affect damage, but aphid attack increased the susceptibility to mildew. The phloem is the major element attacked. Penetration of the stylets is both inter- and intracellular.

Ashe, G. H. (1947). '*Cantharis cryptica* sp.n. (Col., Cantharidae), a British species new to science.' Ent. Mon. Mag. 83: 59.

This beetle is recorded from Herts, Kent, Suffolk, Essex, Hants, Berks, Surrey, Devon, Cheshire and Staffordshire. *C. pallida* with which it was formerly confused appears to be rarer.

Beirne, B. P. (1947). 'The origin and history of the British Macro-Lepidoptera.' Trans. R. Ent. Soc. Lond. 98: 273–372.

Seeks to answer the questions how and why each species first became established in the British Isles, why each species has its own particular type of distribution, why many species are represented by local races, and gives information concerning the histories of the species subsequent to their establishments.

Blackie, J. E. H. (1946). 'Butterflies of a Manchester housing estate.' Northw. Nat. 21: 185–7.

A discussion of the status of 16 species observed during the past 10 years on a housing estate with small woods, pasture land and market gardens on heavy soil, mostly clay. *Polyommatus icarus* was recorded only in 1937.

Broadbent, L. & Hull, R. (1947). 'Aphides in root clamps.' Agriculture, 54: 319–22.

The peach-potato aphis and the tulip aphis were found in many mangold clamps. Neither of these species was found in swede clamps, but shallot aphis was.

Bromley, P. J. (1947). 'Biological observations on *Chrysomela tremula* F. (Col., Chrysomelidae) at Oxford.' Ent. Mon. Mag. 83: 57–8.

Eggs laid in small clusters on aspen. Larvae possess scent glands which seem to repel spiders. When full fed they leave the food plant and pupate head downwards on low herbage. The larval skin which remains on the pupa appears to retain the larval scent. The adults give off a poppy-like scent and if disturbed drop off the leaf to the ground and remain with dark underside uppermost. One larva was parasitized by a tachinid fly.

Clark, R. B. (1947). 'Seasonal fluctuations in the song of the sky-lark.' Brit. Birds, 40: 34–43.

Records of the singing of single birds throughout the season show peaks in autumn and late winter—early spring with smaller peaks continuing into the summer. Closer analysis shows a probable relation of these last to phases of the breeding cycle.

Collinge, W. E. (1946). 'Some observations on certain terrestrial Isopoda.' Northw. Nat. 21: 224–26.

The author concludes from observations over more than 30 years that *Oniscus asellus*, *Porcellio scaber* and *Armadillidium vulgare*, the three commonest and most widely distributed species, are successful owing to their ability to adapt themselves rapidly to new surroundings and survive for long periods with little food and to their fertility, effective system of aerial respiration and longevity, which averages over four years.

D'Assis-Fonseca, E. C. M. (1947). '*Dionaea aurifrons* Meig. (Dipt., Larvaevoridae): a genus and species new to Britain.' Ent. Mon. Mag. 83: 133.

Captured 5 August on ragwort at Puttsborough, Devon. Description appended.

Easton, A. M. (1947). 'The Coleoptera of flood-refuse. A comparison of samples from Surrey and Oxfordshire.' Ent. Mon. Mag. 83: 113–15.

Comparison of a sample of flood refuse from the River Mole, at Mickleham, Surrey, 25 November 1946, with one from the River Thames at Shillingford, Oxon. The former contained 152 species, the latter 272, out of a total of 327 species.

Edwards, G., Hosking, E. & Smith, S. (1947). 'Aggressive display of the ringed plover. (Studied by means of a stuffed specimen and a mirror.)' Brit. Birds, 40: 12–19.

A study of the various postures and actions elicited with a stuffed bird and with a mirror. Twelve excellent half-tone illustrations are included.

Elton, C. (1947). 'Some Orthoptera from Shropshire and Pembrokeshire.' Ent. Mon. Mag. 83: 42.

On Whixall Moss, Shropshire, *Metrioptera brachyptera* (not recorded by Burr), *Myrmeleotettix maculatus*, and *Chorthippus parallelus* were taken under damp heath conditions. In Pembrokeshire, *Platycleis occidentalis*, *Chorthippus bicolor* and *C. parallelus* were taken in maritime cliff vegetation on Marloes Sands. The two latter were also caught at Dale, while the former is a new record and appeared to be at the northern point of a range bounded by the zone of average high temperature 40–50° F. as is the case for the house spider *Pholcus phalangioides* (seen at Dale). *Tettigonia viridissima* was also taken near Marloes, further west than is recorded by Burr for Wales (Burr, M. (1936) 'British Grasshoppers and their allies').

Evans, A. C. & Guild, W. J. McL. (1947). 'Studies on the relationships between earthworms and soil fertility. I. Biological studies in the field.' Ann. Appl. Biol. 34: 307–30.

Temperature and moisture are two soil conditions which determine changes in the seasonal activity of various species. Two species have an obligatory diapause, while changes in population have been noted in two other species. Soil temperature and moisture also determine the weight of soil thrown up as worm-casts during autumn, winter and spring. Only two species appear to be responsible for worm-casts. The previous agricultural history of the field is important in determining the earthworm fauna, so is soil type. Thus the dominant species of pasture land at Rothamsted was *Allolobophora nocturna*, which was not found in the Carse of Stirling.

Gough, H. C. (1947). '*Galeruca tanaceti* L. (Col., Chrysomelidae) in unusually large numbers.' Ent. Mon. Mag. 83: 15.

Very large numbers appeared on *Centaurea nigra* at Knaresborough, Yorks. These had almost disappeared by 11 October, 1946, and there were no signs of the beetle sheltering at the root of the plant.

Gough, H. C. (1947). 'A note on the occurrence in Yorkshire of *Celaena* (=*Apamea*) *secalis* L. (Lep., Caradrinidae), *Opomyza germinationis* L. (Dipt., Opomyzidae) and *Crepidodera ferruginea* Scop. (Col., Chrysomelidae) in winter wheat.' Ent. Mon. Mag. 83: 130.

Apamea seems to favour medium and heavy soils, *Crepidodera*, light soils. *Opomyza* appears to occur on heavy soils after cereals, but it is not affected by soil conditions after seeds. All occur mainly on wheat after seeds or cereal crops.

Grensted, L. W. (1947). 'Diptera in the spathes of *Arum maculatum* L.' Ent. Mon. Mag. 83: 1–3.

Psychoda phalaenoides and *P. grisescens* (Psychodidae) were dominant. *Limosina* sp. (Sphaeroceridae) were attracted to the flowers, but not on a scale important for their pollination.

Grensted, L. W. (1947). 'Some notes on the British Oscinellinae (Dipt., Chloropidae).' Ent. Mon. Mag. 83: 54–5.

Records of 19 species.

Hill, M. A. (1947). 'The life-cycle and habits of *Culicoides impunctatus* Goetghebuer and *Culicoides obsoletus* Meigen, together with some observations of the life-cycle of *Culicoides odibilis* Austen, *Culicoides pallidicornis* Kieffer, *Culicoides cubitalis* Edwards and *Culicoides chiopterus* Meigen.' Ann. Trop. Med. Parasit. 41: 55–115.

A very comprehensive account of the rearing of *C. impunctatus* and *C. obsoletus* both in the laboratory and field and of their habits and incidence throughout a complete year, with similar but less complete observations on *C. odibilis*, *C. pallidicornis*, *C. cubitalis* and *C. chiopterus*. *C. impunctatus* normally passes through one generation per year the peak period for adults being June, and lays one batch with an average of 50 eggs. *C. obsoletus* has two generations with peaks in June and end of September and lays one batch with an average of 75 eggs. The number of adults emerging from eggs transferred to the breeding pots was 15%, 20% for *C. impunctatus*. An illustrated account is given of the morphology of adult and immature forms of all species. The literature is reviewed.

James, A. F. & Webb, J. A. (1945). 'The birds of Swansea borough.' Proc. Swansea Sci. and Field Nat. Soc. Vol. 2, pts. 6 and 7: 212–21.

Swansea Borough covers 24,241 acres of which little more than one-third is built over. Remainder includes very varied country—marsh, wood, commons, meadows, canals, river, sandy shore and cliffs. The list records 75 breeding and 58 non-breeding species, with notes on status and history.

Kaufmann, R. U. R. (1947). 'British Longicorn (Col.) records.' Ent. Mon. Mag. 83: 34–7.

Records of the occurrence of 42 species in 1946 together with notes on abundance and habitat. *Asemum striatum* was captured at Rudheath, Cheshire.

Kaufmann, R. V. (1947). 'Notes on *Grammoptera holomelina* Pool and the colour forms of *G. ruficornis* F. (Col., Cerambycidae).' Ent. Mon. Mag. 83: 10–12.

Key to differences between *G. holomelina* and colour varieties of *G. ruficornis*, with distribution maps.

Lloyd, L. C. (1945). 'The evening flight of the pipistrelle bat.' Trans. Caradoc and Severn Valley Field Club, 11 (1942), 259–64.

Observations made during the four months June–September in two successive years (1940–41). Times of bats' first appearances ranged from 1 to 43 min. after sunset, with average of 27·5 min.; standard deviation 7 min. A correlation table of the two sets of times gave a correlation coefficient of 0·9916. Brief notes on meteorological influences—barometric pressure, temperature, humidity, cloud and wind; and on seasonal variations in time of emergence.

O'Rourke, F. J. (1947). '*Lasius* spp. (Hym., Formicidae) swarming at Cambridge.' Ent. Mon. Mag. 83: 41–2.

On 4 August 1946, at Parker's Piece, Cambridge, swarming began at 2.20 p.m. (G.M.T.) at 67° F. plus a barometric pressure of 29·60 in. Males constituted 90% of the swarm at 2.20 p.m. By 6.0 p.m. the swarm was almost entirely de-alated females at a density of about 4 per sq. yd. Of 38 ♀♀ taken, 24 were *L. niger*, 14 *L. flavus*.

P(arrinder), E. R. (1945). 'London bird life and the flying bomb attacks.' London Bird Report for 1944, No. 9: 28.

Records a small number of instances of disturbance of birds by flying bombs. Such disturbances were purely temporary.

Potts, G. (1946). 'Shropshire butterflies.' Northw. Nat. 21: 251–2.

A list of 40 species found mostly in the Benthall and Broseley districts with indications of abundance in most cases, and localities and dates in some.

Ross, J. (1946). 'Cynipid flies and galls on oak.' Lond. Nat. No. 25 for 1945: 31–46.

Summarizes the results of several years' experimental work by members of the Plant Galls Section of the London Natural History Society in breeding the Cynipidae which gall *Quercus robur* and *Q. petraea*.

Whellan, J. A. (1946). 'The large heath, *Coenonympha tullia*, Müll., in W. Lancashire.' Northw. Nat. 21: 252.

Considerable numbers of the typical subspecies (*tullia*) were observed on moorland characterized by *Betula*, *Calluna*, *Eriophorum angustifolium* and *E. vaginatum* in west Lancashire in June 1946. This subspecies, which occurs in Westmorland and farther north, was formerly fairly common on mosses in south Lancashire and Cheshire, but seems to have been absent in recent years. The mosses are mostly near large towns.

(*d*) Small islands

Harrison, J. M. (1947). 'Some remarks on *Fringilla coelebs* Linnaeus.' Ibis, 89: 411–18.

In western Europe this species is considered to be distributed in a cline from north to south-west marked by decrease in red-brown and increase in bluish colour. British races are darker. There is a discussion on the taxonomy of the races.

Harrison, J. W. H. (1947). 'Three plume moths new to the Hebrides.' Ent. Mon. Mag. 83: 3.

Alucita tetradactyla, *Pterophorus monodactylus* (Lep., Pterophoridae) and *Orneodes hexadactyla* (Lep., Orneodidae) were taken on the Isle of Rhum.

Harrison, J. W. H. (1947). '*Aulacaspis rosae* Bouché and *Lecanium capreae* L. (Hem., Coccidae) recorded for the first time from the Outer Hebrides.' Ent. Mon. Mag. 83: 3.

The former is also a first record for Scotland.

Harrison, J. W. H. (1947). 'The Cecidomyiidae (Dipt.) attached to meadow sweet, (*Spiraea Ulmaria* L.) in the Outer Hebrides.' Ent. Mon. Mag. 83: 99.

Perrisia ulmariae and *P. rostrupiana* new records for Outer Hebrides (S. Uist).

Le Quesne, W. J. (1947). 'Two additions to the list of Jersey Butterflies.' Ent. Mon. Mag. 83: 134.

The skipper, *Heteropterus morpheus* (new to Britain), and the ringlet, *Aphantopus hyperantus*, new to Jersey.

Smith, F. W. (1947). *Hepialus humuli* (L.) var. *thulensis* (Newman) (Lep., Hepialidae) in Dumfriesshire.' Ent. Mon. Mag. 83: 28.

A record of the Shetland race for the Scottish mainland.

Venables, L. S. V. & Venables U. M. (1947). 'Jackdaws breeding in the Shetland Isles.' Brit. Birds, 40: 140–2.

This species has been known to breed in Shetland only for the last few years and an account is given of the breeding history of five pairs traced in 1946.

2. GENERAL REPORTS AND TAXONOMIC STUDIES OF USE TO ECOLOGISTS

Cooper, B. A. (1947). 'The larva of *Agriotes pallidulus* Ill. (Col., Elateridae.)' Ent. Mon. Mag. 83: 43–4.

Figures and description of the larva of *A. pallidulus* with key to differences between this and the larger *Agriotes* spp.

Ford, R. L. E. (1947). 'The use of common salt for keeping down vegetable and other moulds during breeding experiments.' Proc. R. Ent. Soc. Lond. (B), 22: 86–8.

Data showing the strength of solution to be used.

Hincks, W. D. (1947). 'A simple method of pH determination.' Ent. Mon. Mag. 83: 40.

Describes a system of measuring pH by the comparison of test papers with coloured standards.

Kay, G. T. (1947). 'The glaucous gull in winter.' Brit. Birds, 40: 369–73.

A careful study of the plumages and distinguishing characters of this species made in Shetland and illustrated with 16 half-tone plates showing living birds.

Sheerpeltz, O. (1947). 'A British and continental species of *Autalia* Mannerh. (Col. Staphylinidae) new to science, with a key to Palaearctic species of the genus.' Ent. Mon. Mag. 83: 104–7.

Talbot, G. (1947). 'A little-known method for preserving larvae of Lepidoptera and other insects in the dry state.' Ent. Mon. Mag. 83: 152.

Redescribes Tillyard's method of first fixing the larvae in Bie's fixative (alcoholic formol-acetic), dehydrating and clearing in xylol and allowing the xylol to evaporate. Colours are little altered, save green.

Williams, C. B. (1947). 'The logarithmic series and its application to biological problems.' J. Ecol. 34: 253–72.

The paper gives an account of the logarithmic series and its properties, describes methods of fitting a logarithmic series to known data, and summarizes some biological applications. A summary is given of the formulae connected with the logarithmic series.

3. PARASITES

Arthur, D. R. (1947). 'Observations on *Ixodes hexagonus* Leach, 1815 (Acarina: Ixodidae).' Ent. Mon. Mag. 83: 69–76.

Three hosts are needed to complete the life cycle. The most common hosts are *Erinaceus europaeus* and *Mustela* spp. The distribution appears to depend on a suitable host with a tendency to make a permanent home. Two cases of attack in man are discussed.

Crofton, H. D. (1947). 'The parasites of some littoral fishes of Northumberland.' Rep. Dove Marine Lab. 9: 59–64.

Fishes from the littoral zone were examined for parasites. Nine species of trematodes, two cestodes, two nematodes, and one acanthocephalan were found. The importance of size or age of the individual hosts in relation to estimates of incidence is stressed.

[Day, C. D. (1946). 'British Tachinid Flies, Tachinidae (Larvaevoridae).'] Northw. Nat. 21: suppl. 33–64.

This second part of a key to the British tachinids (Northw. Nat. 21: suppl. 1–32, 1946) completes the key to the author's second primary group of genera and contains those to groups 3–19 and the beginning of group 20.

Killington, F. J. & Bathe, E. C. (1947). 'Acarine parasites of Odonata. II—*Arrhenurus leucharti* Piersig, *A. ornatus* George, *A. neumani* Piersig and *Arrhenurus* sp.? nov.' Ent. Mon. Mag. 83: 116–24.

The larvae parasitize dragonflies, first attaching themselves beneath the wing rudiments of the last instar nymph and transfer themselves to the wing veins of the imago on its emergence from the nymphal skin. The nymphal and adult mites are predacious and aquatic. How they return to the water after they leave the hosts is not known. Distribution and host records are given.

Killington, F. J. & Bathe, E. C. (1947). 'Acarine parasites of Odonata. III—*Limnochares aquaticus* (Linnaeus).' Ent. Mon. Mag. 83: 145–7.

The larvae are primarily parasitic on Gerridae, but have been found on adult dragonflies. These are probably parasitized by direct contact in the adult stage, e.g. during oviposition. *Lestes sponsa* (Odonata) which oviposits well above the surface of the water and holds its body away from its support when at rest, was not [illegible]. *Epithemis*, *Palaeobasis*, and *Enallagma* all hold tightly to the support and oviposit near to or below the surface of the water.

MacLeod, J. (1947). 'The climatology of blowfly myiasis. I. Weather and oviposition.' Bull. Ent. Res. 38: 285–303.

Correlation of oviposition with air temperature and inversely with saturation deficiency.

Morgan, D. O. & Sloan, J. E. N. (1947). 'Researches on helminths in hill sheep: with special reference to seasonal variations in worm egg output.' Scot. Agric. 27: 28–35.

There is a very marked increase in output of eggs during the spring, lowest levels occurring during the winter months.

Werth, I. (1947). 'The growth of a young cuckoo.' Brit. Birds, 40: 331–4.

Daily weights throughout fledging are given for three young cuckoos. One which was reared in a wet season grew somewhat more slowly and fledged at a weight of 15 g. less than the other two.

Wright, D. W., Geering, Q. A. & Ashby, D. G. (1947). 'The insect parasites of the carrot fly, *Psila rosae*, Fab.' Bull. Ent. Res. 37: 507–29.

Life history, development and host relations of the Braconid *Dacnusa gracilis* and Proctotrupoid *Loxotropa tritoma* with notes on their distribution and range of parasitism. Larval stages of the Staphylinid beetle *Aleochara sparsa* are described. Brief reference is made to the Cynipoid *Kleidotoma* sp.

4. FOOD AND FOOD HABITS

Brown, W. W. & Cheng, C. (1946). 'Investigations into the food of the cod (*Gadus callarias* L.) off Bear Island, and of the cod and haddock (*G. aeglefinus* L.) off Iceland and the Murman coast.' Hull Bull. Mar. Ecol. 3, No. 18: 35–71.

At Bear Island cod mostly ate pelagic Crustacea between February and August and young herring from November to December.

Campbell, J. W. (1947). 'The food of some British wildfowl.' Ibis, 89: 429–32.

Summaries of stomach contents are given for a number of species of duck and geese. Most of the data are for grey-lag goose (11 specimens), mallard (27), teal (25), tufted duck (8), golden-eye (6) and red-breasted merganser (7).

Ellison, N. F. (1946). 'Weasel caught in mole's run.' Northw. Nat. 21: 246–7.

The weasel (*Mustela nivalis*) had crawled along the mole's run, which was 2–3 in. below the surface, for 30½ yd. before entering the trap. Mice, voles and rats comprise the chief food of weasels, and the mole-catcher who reported the occurrence had not previously found a weasel in a mole's run in many years' experience.

Ellison, N. F. (1946). 'Kestrel devouring prey whilst flying.' Northw. Nat. 21: 248.

The kestrel (*Falco tinnunculus*) rose to a height of about 100 ft., carrying its prey in its left foot, and then circled while eating it, still held in its claws.

Hartley, P. H. T. (1947). 'The natural history of some British freshwater fishes.' Proc. Zool. Soc. Lond. 117: 129–206.

A very long and detailed paper dealing with British 'coarse' fish. Attention is concentrated on distribution of size groups, the validity of scale readings as age indicators and the analysis of stomach contents from different parts of the country.

Jacob, F. H. (1947). 'An account of a black aphid, *Doralis fabae* (Scop.) subsp. *armata* (Hausmann), found on *Digitalis purpurea*, L.' Bull. Ent. Res. 37: 431–7.

The following species of ant attend this aphid: *Formica fusca*, *Acanthomyops flavus*, *A. niger*, *Myrmica ruginodis* and *M. laevinodis*. Syrphids, cecidomyid larvae and thrombid mites are predators. A braconid parasite, *Aphidius* (*Lysiphlebus*) *dissolutus*, wiped out the colonies at one station.

Ogilvie, C. M. (1947). 'Observations in a rookery during the incubation period.' Brit. Birds, 40: 135–9.

Continuous observations on a group of eight nests for 8 hr. showed that incubation by the females was very assiduous and that they got their food almost entirely from the males. Thus from checks at 5 min. intervals males were present 198 times out of a possible 324 and females 276 times.

Rogerson, J. P. (1947). 'The oat bird-cherry aphis, *Rhopalosiphum padi*, L., and comparison with *R. crataegellum*, Theo. (Hemiptera, Aphididae).' Bull. Ent. Res. 38: 157–76.

Includes notes on the biology and food plants of these two aphids.

Sankey, J. H. P. (1947). 'Humus as a possible food of wireworms (larvae of *Agriotes* spp.) (Col., Elateridae).' Ent. Mon. Mag. 83: 20–2.

Larvae were placed in tubes containing soil plus humus stained with trypan blue. Only two out of 112 larvae fed. Thus wireworms do not seem to use plant humus as food.

Stokes, H. G. (1947). 'Observations on the juniper bug, *Pitedia juniperina* L. (Hem., Pentatomidae).' Ent. Mon. Mag. 83: 14–15.

Various plants were offered to a single male. The most favoured food plants were: *Syringa*, *Ulex*, *Fraxinus*, and *Ligustrum*. No attempt was made to eat other small arthropods. Juniper was attacked on one occasion only and was abandoned for lilac.

Thomas, D. C. (1947). 'Some observations on damage to potatoes by slugs.' Ann. Appl. Biol. 34: 246–51.

The garden slug, *Arion hortensis*, and the keeled slugs, *Milax* spp., are the species mainly responsible for potato tuber damage in south-west England. Significant differences in varietal attack is demonstrated, Arran Banner was the most damaged variety, Arran Peak the least and Majestic intermediate. Varietal differences are associated with differences in the dates of maturity, little damage occurring prior to the maturing of the tuber.

Walshe, B. M. (1947). 'Feeding mechanisms of *Chironomus larvae*.' Nature, Lond. 160: 474.

Chironomus plumosus attaches a conical web made from strands of saliva across the inside of its U-shaped burrow. By undulating its body the larva creates a current through the burrow, then eats the web and contents filtered from the water.

5. POPULATION STUDIES

Alexander, W. B. (1945–47). 'The woodcock in the British Isles.' Ibis, 87: 512–50; 88: 1–24, 159–79, 271–86, 427–44; 89: 1–28.

This long report contains much information on all aspects of the woodcock's biology obtained by means of a questionnaire circulated by the British Trust for Ornithology in 1934. The results fall under the following headings: distribution in the breeding season (showing extension of breeding range in last century), habitat, fluctuations in numbers, clutch and brood size, variation in size and colour, migration and winter distribution (with a summary of game bag records). There is an extensive bibliography.

Alexander, W. B. (1947). 'The index of heron population, 1946.' Brit. Birds, 40: 204–7.

There was little change in the breeding population of herons in Britain between 1945 and 1946.

Alley, R. & Boyd, H. (1947). 'The hatching and fledging success of some coot.' Brit. Birds, 40: 199–203.

Observations during a single breeding season showed a loss of 79 out of 121 eggs (65%), the main cause being predators, including carrion crows and man. Of the 42 young 28 (67%) were fledged. Chick mortality was severe during the first few days after hatching due mainly to attacks by adults other than the parents (there were no pike in the lake), but comparatively light afterwards.

Barnes, H. F. (1947). 'Periodic fluctuations in the prevalence of the wheat blossom midges.' J. Anim. Ecol. 16: 74–5.

A table shows the number of larvae of *Sitodiplosis mosellana* and *Contarinia tritici*, separately and together, found in 500 ears of wheat from 1927–46 inclusive, as well as the corresponding percentage grain attack. A diagram shows the peak years as observed previous to 1927 and the total numbers of larvae found in the Broadbalk investigation during 1927–46. Two large peaks, in 1931 and 1946, are shown, and two minor ones in 1935 (?1936) and 1941.

Boyd, A. W. (1946). 'Early natural history records in Cheshire and Lancashire.' Northw. Nat. 21: 227–33.

These records of 18 birds regarded as pests taken from churchwardens' accounts in the sixteenth to nineteenth centuries conclude an earlier list.

Cramp, S. (1947). 'Notes on territory in the coot.' Brit. Birds, 40: 194–8.

Observations for two years at St James' Park, London, showed that there was keen competition for breeding territories at suitable parts of the lake especially round the islands, but there was much neutral ground. Fights were very frequent: territories which were maintained at about 1 acre provided adequate breeding facilities, but smaller ones sometimes had to be abandoned.

Crombie, A. C. (1947). 'Interspecific competition.' J. Anim. Ecol. 16: 44–73.

This comprehensive paper deals with factors governing population growth in general, factors tending to reduce competition, and consequences of interspecific competition, and goes on to give examples of interspecific competition in experimental cultures and in the field, ranging from plant micro-organisms to vertebrates. Differences in distribution, structure, and habits attributable to competition are discussed. Two hundred and eighty two references are given.

Ellison, N. F. & Johnston, T. L. (1946). 'Notes on double brood of heron.' Northw. Nat. 21: 247–8.

Ardea cinerea is generally single-brooded, but in 1944, when the first brood had left the nests in a heronry near Carlisle by 26 April, young were again present in two nests on 6 and 27 July. In 1945, newly hatched young were present in two nests on 27 June and were still there on 31 July. In 1943, young in the nests in the first week of September were able to fly by the 11th, and one nest contained young on 14 August, 1946.

Farran, G. P. (1944). 'The herring fishery in Éire, 1921–41.' J. Dep. Agric. Éire, 41: 229–62.

The total catch in cwt. of herrings from 1921 to 1938 shows a rapid rise from 1923 to 1927, about 100,000 to 330,000 cwt., a somewhat similar decrease from 1927 to 1930 with a further decrease from 1930 to 1932 to about 40,000 cwt. and till 1938 fluctuates between about 40 and 70,000. The largest catches were landed on the north-west and south-east coasts. Larger catches are landed during the summer months on the south coast, during autumn and winter along the south-west, autumn, winter and summer along the north-west and usually in the winter along the east coast.

Gough, H. C. (1947). 'Studies on wheat bulb fly, *Leptohylemyia coarctata*, Fall. II. Numbers in relation to crop damage.' Bull. Ent. Res. 37: 439–54.

A detailed quantitative study of the incidence and development of an attack of wheat bulb fly on a field in East Yorkshire. Up to nearly 600,000 larvae per acre occurred. A technique for estimating the number of eggs in the soil is described: over 7½ million eggs per acre were laid in one potato field. The possibility of using egg counts to forecast outbreaks is discussed but not considered likely to be successful.

Gray, R. A. Harper, Peet, W. V. & Rogerson, J. P. (1947). 'Observations on the chafer grub problem in the Lake district.' Bull. Ent. Res. 37: 455–68.

Contains notes on the life history and distribution. The grubs are often most numerous where the gradient increases. Estimates gave 113,520 grubs per acre on the fell-side and 67,207 per acre on the level portion. The number of grubs per acre is lower than when conditions are excessively wet or excessively dry.

Keighley, J. & Lockley, R. M. (1947). 'Fledging-periods of the razorbill, guillemot and kittiwake.' Brit. Birds, 40: 165–71.

Apart from the fledging period data there is some information on fledgling mortality.

Lack, D. (1947). 'The significance of clutch-size.' Ibis, 89: 302–52.

A wide survey, mainly of western European birds, shows that in all passerines and in many other orders of birds clutch-size increases from south to north and from east to west, though this may be slightly complicated by variations due to season and age. It is suggested that in such groups clutch-size is adjusted by natural selection to produce the greatest number of young, which the parents can fledge in a reasonable condition.

Lack, D. (1947). 'The significance of clutch-size in the partridge (*Perdix perdix*).' J. Anim. Ecol. 16: 19–25.

Clutch-size (varying from 10–20, average 14·6 eggs, first layings, in England) is considered to be selected through the food available for the brood, and a method of proving this is suggested.

Mason, A. G. (1947). 'Territory in the ringed plover.' Brit. Birds, 40: 66–70.

Observations showed that the breeding territory was of the order of 30 yd. sq. and that this was defended against all species of intruders. A tendency by neighbouring males to form loose flocks was noted when there was a general disturbance of the nesting area.

May, D. J. (1947). 'Observations on the territory and breeding behaviour of the willow-warbler.' Brit. Birds, 40: 2–11.

Detailed work upon an area of 15 acres of common, 11½ of which were distributed among 33 willow-warbler territories. Data are given on establishment of territory, courtship and general breeding habits, including hatching and fledging success.

Norris, C. A. (1947). 'Report on the distribution and status of the corn-crake. [Part Two. A consideration of the causes of the decrease.]' Brit. Birds, 40: 226–44.

This follows a previous communication which gave figures for the decline in corn-crake numbers in the last few decades. It makes a careful analysis of the factors responsible for the change. The main ones are shown undoubtedly to be the introduction of the mowing machine and the earlier time of hay making.

Rae, K. M. & Rees, C. B. (1947). 'Continuous plankton records: the Copepoda in the North Sea, 1938–39.' Hull Bull. Mar. Ecol. 2, No. 11: 95–132.

Analysis of distribution along ten steamship routes showed a rapid population increase in April or May from a sparse winter population. 'Exotic' copepods may be used as an indicator of water movements, given good knowledge of the plankton composition at the water's source.

Reynoldson, T. B. (1947). 'An ecological study of the Enchytraeid worm population of sewage bacteria beds.' J. Anim. Ecol. 16: 26–37.

A weekly sampling technique was used on the Huddersfield Corporation sewage bacteria beds, and gave information on *Lumbricillus lineatus* (scarce) and *Enchytraeus albidus*, the latter having its main breeding season from October to April inclusive.

Rothschild, M. (1947). 'The wood-pigeon (*Columba palumbus* L.) on the poultry market: preliminary note.' Ibis, 89: 611–15.

Contains an analysis of market figures between 1944 and 1946. An estimate puts the numbers received by the London market only at half a million in 1944 and three-quarters of a million in 1946. Monthly returns show a peak in March–early April, which is probably because birds react much better to decoys at this period.

Solomon, M. E. (1947). 'Mortality required to prevent population increase.' Nature, Lond. 159: 848–9.

In certain calculations of the 'necessary mortality' which will keep a fecund population at a constant density there is a striking fallacy which appears in papers of some importance to insect population studies. Formulae are used which imply that there is no mortality (except of adults after reproducing) in the series of generations under consideration.

Storrow, B. (1947). 'Concerning fluctuations and the teaching of ecology.' Rep. Dove Marine Lab. 9: 7–58.

Study of physiology, meteorology and hydrography is valuable in the training of marine ecologists. Changes in weather and climate are linked with some recent fluctuations in marine populations. The historic environment, ice, periodicities and some North American fluctuations are dealt with, as well as a section on historic fluctuations which includes records of whales, salmon, grilse, herring, pilchard, tunny, cod, and records of rare fish. Ninety-eight references are given.

Tooby, J. (1947). 'Notes on sand-martins.' Brit. Birds, 40: 290–7.

Observations are given on the number and size of colonies along some 39 miles of river from 1942 to 1944. In this short period there was no great variation in total breeding numbers but groups frequently shifted their positions. Nesting behaviour and courtship are described.

Went, A. E. J. (1946). 'The Irish pilchard fishery, the possibility of revival.' J. Dep. Agric. Éire, 43: 48–51.

From 1611 to 1689 there was a flourishing fishery along the south coast but since then shoals have shown considerable irregular fluctuations and it is doubtful if there could be a profitable revival of the industry.

Went, A. E. J. (1947). 'Salmon of the Kerry Blackwater.' Sci. Proc. R. Dublin Soc. 24: 179–87.

Gives tables for the distribution of the various age groups; size, weight and length distributions; proportion of spring and summer fish; mean condition coefficients and condition factors; fluctuations in the annual catches in the Kerry Blackwater and River Ballisodare which show marked similarity between the curves drawn for the numbers representing ten-year averages.

Went, A. E. J. (1947). 'Irish Salmon, 1945.' Sci. Proc. R. Dublin Soc. 24: 165–78.

8,300 fish were examined from 25 rivers. Most smolts were from the two-year-old age group with the first and third year groups next in order of abundance. 49·7% of the fish were less than a full year at sea and spawned after their first winter, 46·3% spent a full year at sea and spawned in their second winter. The average proportion of previous spawners was 5·4%; 93% had one spawning mark, 6·5% two and 0·5% three.

Williams, C. B. (1947). 'The generic relations of species in small ecological communities.' J. Anim. Ecol. 16: 11–18.

It is possible to compare the Index of Diversity in natural small or simple ecological communities with that of the larger population from which these have been selected by nature. The results from using this method indicate that there is a selection by nature in favour of more than one species in the same genus rather than in favour of single species in different genera.

Williamson, K. (1946). 'Field-notes on the breeding-biology of the whimbrel, *Numenius phaeopus phaeopus* (Linnaeus).' Northw. Nat. 21: 167–84.

The subjects dealt with in these studies, made in the Faroe Islands, are nesting sites, clutch size and nesting success, incubation and hatching periods, the development and movements of unfledged chicks and the behaviour of the chicks, courtship, sitting habits, attendance on young, distraction displays by the adults, and call notes.

6. MIGRATION, DISPERSAL AND INTRODUCTIONS

Allen, A. A. (1947). '*Dorytomus filirostris* Gyll. (Col., Curculionidae), a weevil new to Britain.' Ent. Mon. Mag. 83: 52.

This rare central and southern European species was taken in 1945 on *Populus nigra* at Wicken Fen (Cambs.). Its occurrence in such a well-worked locality is remarkable.

Bartlett, T. L. (1945). 'Movements of tufted ducks ringed in St. James's Park.' London Bird Report for 1944, No. 9: 22.

Summarizes the ringing returns, showing that many birds return to the same spot in following winters.

Blair, K. G. (1947). 'Cosymbia pupillaria Hübner (Lep., Sterrhidae) in the Isle of Wight.' Ent. Mon. Mag. 83: 29–30.

A single ♀ of this southern European species was taken near Freshwater. Previously recorded from Scilly. It may be a recent immigrant or have been introduced with exotic shrubs. Adult, eggs, and first stage larvae described.

Campbell, J. W. (1947). 'Notes on the birds of Abberton reservoir, Essex.' Brit. Birds, 40: 79–82.

Notes on the populating of a new reservoir first filled in 1939.

Ellison, N. F., Burd, A. C. & Jones, P. (1946). 'Bee-eaters in Lancashire.' Northw. Nat. 21: 248–9.

Two *Merops apiaster* in winter plumage were observed in gardens near Southport on 8–10 October 1946. They returned on 19th, and at the time of writing had been there for over a fortnight, despite a persistent east wind, evidently because at least three gardens contained bee-hives. They were generally attacked by other birds when in flight, but during their first visit were observed to fly unmolested with starlings. There appears to be no previous record of this bird from Lancashire, or from Cheshire.

Gibb, J. & Tucker, B. W. (1947). 'The exceptional passage of curlew-sandpipers and little stints in the autumn of 1946.' Brit. Birds, 40: 354–9.

Glegg, W. E. (1947). 'Remarkable spring migration at Tring reservoirs.' Brit. Birds, 40: 107–8.

Large numbers of waders and gulls were recorded passing through this inland station during late April and May of 1946 during a period of sustained north-east winds.

Jackson, L. H. (1946). 'Pilot whales on the North Wales coast.' Trans. Anglesey Antiq. Soc. and Field Club, 1945: 67–72.

Records stranding of about 20 *Globicephala melaena* on 31 August and 1 September 1945, in and around Conway estuary, after strong gale. Of 9 males and 7 females measured, longest was 20 ft. 1 in., smallest 8 ft.

Gut of those examined contained no food. Body cavities of several contained tapeworm larvae, probably *Phyllobothrium*; a Nematode parasite present in numbers in the extensions of tympanic cavity of ear. Notes on blubber, glottal plug, pelvic bones, etc.

Parrinder, E. R. (1947). 'The little ringed plover in the London area in 1946.' Brit. Birds, 40: 109–11.

Four pairs of this species—only recently added to the British breeding list—were recorded on gravel pits around London in the 1946 season.

Roebuck, A., Broadbent, L. & Redman, R. F. W. (1947). 'The behaviour of adult click beetles of the genus *Agriotes* (*A. obscurus* L., *A. lineatus* L., and *A. sputator* L.).' Ann. Appl. Biol. 34: 186–96.

Descriptions of various trapping methods. A 3 in. thickness of hay over closely clipped grass is suitable for population and movement studies in grass fields. Annual and daily activity are discussed. Movement is almost entirely along the ground or on low plants. Marked beetles were recovered at a maximum distance of 26 yd. from their point of release.

Went, A. E. J. (1947). 'Salmon marking in Ireland.' Proc. R. Irish Acad. B, 51: 173–95.

Some of the marks (metal tags) used were unsatisfactory, so that an accurate figure for the proportion of fish surviving to return as clean fish to the rivers was not obtained. The records provide a minimum figure of 2·22%. Previously spawned fish showed a marked 'homing instinct', some of their routes are indicated. Fish spending a year or more feeding at sea increase in length by 30% and in weight by 130%, those less than a year by 14 and 90% respectively.

Werth, I. (1947). 'The tendency of blackbird and song-thrush to breed in their birthplaces.' Brit. Birds, 40: 328–30.

Analysis of ringing returns shows that the blackbird disperses from its birthplace less than the song-thrush. Of birds recovered breeding away from their birthplaces (over 5 miles distant) the blackbird has 7% and the song-thrush 17%.

Williamson, K. (1946). 'Great and sooty shearwaters north of Orkney.' Northw. Nat. 21: 247.

Puffinus gravis in parties of up to 20 was almost continuously in sight during observations made over a few hours from a ship returning from the Faroe Islands on 17 September 1945. *P. griseus*, singly or in small groups, was less frequent, but still common. All the birds were flying to the south-east.

7. REPORTS OF ORGANIZATIONS

British Trust for Ornithology (1947). Thirteenth Report. 22 pp.

Contains a brief summary of economic work done upon population and feeding habits of the rook, and short paragraphs on various current inquiries.

Freshwater Biological Association of the British Empire (1947). Fifteenth Annual Report for the year ending 31st March, 1947. 51 pp. (Price to non-members, 1*s*. 6*d*. F.B.A., Wray Castle, Ambleside, Westmorland.)

The Director's Report reviews research in hydrology including a study of the distribution of algae and dissolved substances under ice cover, algology, aquatic fungi, bacteriology, invertebrate zoology (investigations on Mollusca and nymphs of Ephemeroptera) and fish—char, pike, trout and perch.